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Pasture soils in the Tropical Moist Life Zone of Costa Rica: implications for secondary forest succession

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by

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GENERAL INTRODUCTION

Dissertation Organization

This dissertation is presented in two main parts. Part I presents results of a field research project conducted in Costa Rica. The project looked at changes in soil characteristics between undisturbed primary tropical forest and pasture land. The first part presented in the dissertation reports on the results of a study conducted from January to March 1993 in the Puriscal region of Costa Rica. This study examined the soil characteristics in paired plots of forest and pasture and discussed these results in relation to changes in soil characteristics in sites that have been converted from forest to pasture. These changes were also related to the impact of cattle on nutrient cycling and erosion in pastures.

Part II presents results of a research project that examined the extent of soil degradation in the pasture soils of the first project using a site-quality assessment model developed by Gutiérrez (1991). The second part uses the data collected in the field study in a site-quality assessment model developed by Gutiérrez (1991). The model was adapted for use in two Life Zones in Costa Rica. The synecological coordinates for forest plots, pasture plots and for plots placed in three erosion classes were calculated and compared.

The dissertation begins with a general introduction, which discusses the overall problem addressed, followed by the literature review. Presentation of the two research projects follows. The dissertation ends with a general summary. Following is the general introduction, including a statement of the overall problem studied in this dissertation.

Soil Degradation

Deforestation of the tropical regions of the Earth is taking place at an alarming rate. Approximately 250,000 square kilometers of tropical forest are either subjected to logging or are converted to other land uses every year (Meyers, 1991; Veldkamp, 1992). In Costa Rica, as of 1984, over 67% of the country had been deforested (Fournier, 1985; Sader and Joyce, 1988). By 1989 the deforested area had climbed to 76% (Solórzano et al., 1991). Large areas of Guanacaste and the Meseta Central have been cleared for many years, but in recent decades deforestation has reached into the highest parts of the mountains and to the lowland rain forests of the east and the southwest of Costa Rica as roads have made these areas accessible.

The underlying reason for deforestation in Costa Rica is the undervaluing of forest resources (Jones, 1992). This undervaluing takes several forms. Forests may have a negative value to farmers because of the tax imposed on underutilized land. Greater value is also placed on cleared land because of the potential loss of "unused" land to invasion by poor farmers. Population pressures also play a part in deforestation by encouraging the settlement of surplus population into forest areas. These areas are seen as potential areas for expansion of farming. The population of Costa Rica doubled from 1.2 million in 1960 to about 2.5 million in 1984 (Fournier, 1985), and there have been several development projects in the Atlantic lowland forests designed to encourage landless farmers to migrate to the region. However, even with the growth in

population, the land area devoted to agricultural crops had only increased 20% in the 35 years leading up to 1985 (Fournier, 1985).

Much of the land cleared of forest during that 35-year period was eventually converted to pasture. During the period when land devoted to agriculture rose 20%, the area devoted to cattle increased by over 100%. Landless farmers would often clear an area that was either in the public domain or was considered "unused" private land and would grow a crop for a few years until the nutrients in the burned slash were gone. The land would then be sold to a rancher and seeded to grass.

The forests converted to cattle production in the recent past have mainly been in mountainous areas where erosion from overgrazing has destroyed a significant portion of the soil resource of the country. Hartshorn et al. (1982) estimated that one quarter of Costa Rica's soil resources had been lightly to moderately eroded by grazing, while a fifth had been severely eroded. Many pastures have been abandoned because of the loss in productivity and the reduction in government subsidies to ranchers in the early 1980's (Solórzano et al., 1991).

These degraded pastures have lost productivity because of accelerated erosion, compaction and loss of organic matter. Some of the degradation is simply a consequence of changes in microclimate that result from the conversion of forest to pasture, such as the loss of organic matter caused by increased soil temperatures near the surface. For example, Lal and Cummings (1979) found that after deforestation in southern Nigeria the maximum air temperature increased by 5-8° C and soil temperatures at 1 cm increased by 25° C.

Aside from the degradation that can result from changes in microclimate, degradation also results from overstocking. Overstocking can cause accelerated erosion through loss of ground cover and by physical disruption of the soil surface by animal hooves (Humphreys, 1991). Compaction can occur if animals are grazed on soils when the soil moisture is at levels favorable to deformation of the soil (Humphreys, 1991) Both of these processes can cause a loss of pasture productivity. Even at lower stocking rates, there can be extensive alteration of the soil. Grazing steps form in most pastures with slopes greater than about 27% from the movement of livestock across the slopes (Howard and Higgins, 1987). Grazing steps can inhibit or accelerate erosion depending on the soil type and the climate. In California, Higgins (1982) noted that grazing steps that developed on a road embankment appeared to inhibit erosion in the Mediterranean climate of that region. Steps that were created in a Great Plains setting appeared to accelerate erosion (Brice, 1958).

Several studies specific to Costa Rica have documented soil changes when forests are cleared. Daubenmire (1972) detected losses in organic matter and significant erosion in pasture soils in the Guanacaste region. Krebs (1975) found in north-central Costa Rica that there were declines in organic matter, nitrogen and pH in soils that had been cleared for crops and pasture for as long as 22 years. In eastern Costa Rica, soils that formed on lahars (volcanic mud flows) changed considerably in as little as 4 years when cleared for crops and pasture (Wielemaker and Lansu, 1991). All of these studies show that rather dramatic changes can occur in Costa Rican soils cleared of forest.

Many pastures in the Puriscal area of Costa Rica have been abandoned as cattle raising has become unprofitable because of lower subsidies or because of

lower pasture productivity resulting from soil degradation. On these abandoned pastures, secondary forest succession occurs. Secondary succession takes place quickly on pastures that have not been degraded. In one 21-year-old abandoned pasture, there were over 50 tree species present, and a ten-year-old site had developed to the point where it had the floristic and structural diversity to support wildlife and protect the soil (Fournier and Herrera de Fournier, 1977). However, on degraded pastures secondary succession is slowed (Fournier, 1990), and the potential growth of the forest is reduced because of nutrient loss and soil compaction (Solórzano et al., 1991).

Understanding and controlling secondary succession on abandoned, degraded pastures is dependent on having a firm foundation of knowledge about the changes in soil characteristics that accompany the degradation process. However, none of the past studies in Costa Rica have looked at soil changes in pastures from the perspective of the impact of soil degradation on secondary forest succession. Two studies in northeastern Brazil have looked at the impact of soil degradation in pastures on regeneration of trees and secondary forest succession (Buschbacher et al., 1988; Uhl et al., 1988). In these studies, pastures were classified into three classes of land use on the basis of the success of pasture establishment, grazing pressure and whether mechanical clearing was used. The studies found that on the most degraded pastures regeneration was impaired. However, the cause of impairment was not low soil productivity, but rather the lack of tree propagules. There was no potential for tree establishment in the degraded pastures because there were no residual roots or seeds.

The present study takes a first step towards understanding how the soil characteristics of pastures in the Puriscal region of Costa Rica impact tree

regeneration by examining how several soil characteristics of pasture soils differ from the soil characteristics of paired undisturbed forest sites. A direct link between soil characteristics and tree regeneration was not attempted. It was believed that with the limited resources available for this study that it was important to first understand how soil characteristics have changed in pastures since the sites were cleared of forest and to identify the level of degradation in these pasture soils. A future exclosure study will examine the link between soil characteristics and tree regeneration.

The first part in this dissertation is designed to examine the changes that have occurred to soils in the Puriscal region of Costa Rica on sites that have been converted from forest to pasture. It also looks at the changes to these soils resulting from overgrazing. Two hypotheses will be tested by this study. The first hypothesis is that clearing an undisturbed tropical moist forest and converting it to pasture will cause soil degradation as shown by reductions in the levels of organic carbon and total nitrogen, increases in bulk density and clay content, and a decrease in soil pH in the surface horizons of soils.

The second hypothesis is that erosion group definitions are related to soil degradation. Erosion group 1, the least eroded group, will have the lowest increase in bulk density and clay content and the lowest decrease in total nitrogen, pH and organic carbon. The other two groups will have changes in soil characteristics proportional to their defined level of erosion.

Site-Quality Assessment

Many pastures in Costa Rica may be degraded to the point that tree regeneration is impeded. Other pastures may be only slightly degraded, while some pastures may not have had any reduction in productivity. If these pastures are abandoned secondary succession begins. On the undegraded pastures, secondary forest succession is not impeded by any soil characteristics. On the slightly degraded pastures, succession proceeds, but the lower site quality causes a shift in species composition to trees that are less sensitive to site quality. Pastures that have been highly degraded have a site quality so low that regeneration by any tree species is difficult. A system of site-quality assessment would be very useful in identifying the various levels of degradation in pastures and would assist landowners in choosing either appropriate species for planting on these sites or in identifying a suitable reclamation technique for increasing site quality.

Site-quality assessment can be evaluated in two basic ways (Husch, Miller and Beers 1982). A vegetation characteristic sensitive to site quality can be measured. The measurement of tree height for site index is an example of this method. A second method relates site quality to environmental site factors that are known to influence site quality. Numerous soil characteristics have been used to develop site quality models for forestry. In this indirect approach, sample locations in a forest population are selected. Then information on site index or tree volume and information on a number of soil characteristics are collected. The soil characteristics are then related to the information on tree

growth by using multiple regression. The resulting equations can then be used to predict site quality on sites that are without forest (Clutter et al., 1983).

The indirect approach to assessing site quality could prove useful in determining if the level of degradation in pastures in Costa Rica limited tree regeneration. It could also be used to select appropriate tree species for pastures that have had only slight to moderate degradation.

As mentioned before, there have been many attempts to develop site-quality models in forestry. Most of these models have been developed for temperate forests. The direct models, such as site index, can be successfully used in the temperate zone but do not work well in the tropics. For example, site index can only be used if the age of the stand is known. Age can easily be measured in temperate forest species that have annual growth rings, but in the tropics tree age cannot be measured using annual growth rings because many tree species lack rings. For tropical forests, site-quality assessment is best done using indirect means. Gutiérrez (1991) and Gutiérrez and Mize (1993) developed a system that uses the method of synecological coordinates (Bakuzis, 1959) to quantify the operational factors (synecological coordinates) of a site and then uses linear regression to link the synecological coordinates to site physiognomic characteristics. The system can be used identify the synecological coordinates of a site using its physiognomic characteristics and also can be used to predict the appropriate tree species to plant on a site.

The first hypothesis of the second research project is that the site-quality assessment model developed by Gutiérrez (Gutiérrez, 1991; Gutiérrez and Mize, 1993) will show that the soils of the pasture plots are degraded when compared to the forest plots, as shown by the pasture plots having lower moisture and

nutrient coordinates in the edaphic field and higher light and heat coordinates in the climatic field than the forest plots.

The second hypothesis is that the Gutiérrez model will show an increasing amount of degradation moving from erosion group 1 to erosion group 2 to erosion group 3, as shown by a decrease in the moisture and nutrient coordinates in the edaphic field and an increase in the light and heat coordinates in the climatic field as erosion increases.

The third hypothesis is that the pasture plots will have impeded tree regeneration compared with the forest plots, as shown by the moisture, nutrient, light and heat coordinates of the pasture plots being outside the boundaries of the ecographs for three selected tropical plant species.

The fourth hypothesis is that there will be an increasing impediment to tree regeneration as erosion increases in the pasture plots, as shown by the moisture, nutrient, light and heat coordinates of the three erosion groups being increasingly outside the ecographs of the three selected tropical plant species as erosion increases from erosion group 1 to erosion group 2 to erosion group 3.

Success or failure of tree regeneration as discussed in all of the above hypotheses and in the following sections refers to success or failure of tree seed germination.

LITERATURE REVIEW

Introduction

The following literature review is in three parts. The first part reviews literature related to forest clearing and pasture grazing and the impact of both activities on microclimate, nutrient cycling, runoff and erosion.

The second part of the literature review will first discuss the operational factors of the environment (water, heat, radiation, oxygen and nutrients) that influence trees. Next the impact of soil characteristics on operational factors will be examined. Finally, a link will be made between operational factors and tree regeneration.

Part three of the literature review surveys literature relating to tree regeneration problems in the tropics.

The Impact of Forest Clearing and Grazing on Soil Characteristics and Tree Seed Germination

Land clearing

Clearing of forests for agriculture has been done in all parts of the world since the start of agriculture thousands of years ago. In many parts of the temperate zone and in some parts of the tropics the native fertility of the land has fostered permanent clearing of forests for agriculture and grazing, while in those parts of the forested tropics with low soil fertility shifting agriculture or some type of agroforestry have predominated. Clearing of forests causes

dramatic changes in the microclimate of the areas cleared. These changes in turn cause changes in the characteristics of the soils of these areas. This section will briefly discuss the general types of forest clearing and how clearing is done under these systems. The type of forest clearing that occurs in the area in Costa Rica examined in this study will also be discussed. The causes of deforestation and land clearing in Costa Rica have already briefly been discussed in the introduction.

Forest clearing can be placed into two broad categories on the basis of the amount of time before the cleared land is allowed to return to forest. Shifting cultivation fits into the category of a temporary clearing. Under this system forest land is cleared and cropped for a few years and then the land is abandoned and the forest grows anew on the site. After a number of years the area is again cleared and cropped for a few years. Shifting cultivation can be sustainable when the fallow period between crops is sufficiently long for the fertility of the soil to return to precrop levels. The length of the fallow varies considerably. Sanchez (1976) notes that fallows can be from 4 to 20 years in length. Under this system changes in soil characteristics are mostly temporary.

Forest is also cleared with the intent of keeping it permanently in another land use. These land uses can be as disparate as clearing for industrial and residential development or clearing for permanent agriculture, arboriculture and grazing. Under this type of clearing changes in soil characteristics can be quite dramatic and long lasting.

Clearing for both temporary shifting cultivation and more permanent land uses can be done using similar techniques. The distinction in techniques is primarily on whether the clearing is done manually or with machines.

Regardless of the source of power used in the clearing, the steps involved in clearing are the same. First the trees and shrubs of the selected area are felled. In some instances the entire area is cleared while in others selected trees are retained. The trees that are retained usually have some value for food, fiber or medicines, though very large trees may present too much effort to fell and may just be girdled.

When trees are manually felled the stumps of the trees are not removed. Planting takes place around the stumps. When machines are used for clearing the stumps are removed and windrowed or pushed into piles. A benefit of this more complete clearing is that machinery can be used in the cropping process.

Once the forest is felled the slash is left to dry. When clearing is done manually the slash is left *in situ* during the drying time. Machinery can be used to push the slash into piles. A problem with concentrating the slash into piles is that organic matter and nutrients are redistributed on the site. Nutrients are removed from a large portion of the site and concentrated in the piles. It is also quite easy for a careless operator of the machinery to scrape off the litter layer and concentrate that organic matter in the piles as well. The uneven distribution of nutrients can cause uneven crop growth. Crops planted where nutrients are concentrated can do extremely well, while crops on the rest of the site will do poorly because of lower nutrient levels there.

In many areas felling is done during the dry season so that rainfall will not slow the drying. However, in some areas drying is not possible because of the lack of a dry season. Snedaker and Gamble (1969) reported that on the Pacific coast of Colombia cleared vegetation was used as mulch because the material could not be dried for burning in the year round rainfall.

Once the felled material is dry it is then burned. The burning has three purposes. First, clearing away the felled vegetation increases access on the site. It is easier to plant, weed and harvest the cleared site. Second, burning the slash prevents it from interfering with the germination of the crops. Third, and most important, the burning speeds the cycling of the nutrients sequestered in the vegetation. Much of the carbon and some of the nitrogen in the vegetation is lost when it is burned, but many of the nutrients are returned to the soil in forms more readily available to the crops (Smith, 1986). Also nutrients that would have been bound up in the vegetation for relatively long periods of time are quickly made available to the crops.

Both shifting cultivation and more permanent clearing occur in Costa Rica. Some shifting cultivation still takes place (especially in the Indian reservations (Solórzano et al.,1991) however, it is mainly a technique of the past. As discussed in the introduction, much of the clearing taking place in Costa Rica today is done with the intention of keeping the land permanently in land uses other than forest. Forest is often cleared and cropped for a few years until the fertility declines then the site is converted to pasture or is used for arboriculture. This change of land use can cause dramatic and relatively long term changes in soil characteristics.

The next section will look more closely at the changes in microclimate that occur when forest is cleared and replaced with pasture. Later the differences between nutrient cycling in forest and pasture will be discussed. Then differences in runoff and erosion between forest and pasture will be examined.

A microclimatic comparison of forest and pasture-cattle systems

Dramatic changes occur to the flow of energy and matter through a system when tropical forests are felled and converted to pasture. Changes in light interception, temperature and moisture have large impacts on the populations of organisms in the system and in the cycling of nutrients. Removal of the forest canopy impacts many of these changes and also influences the runoff and potential soil erosion caused by that runoff. The following sections discuss the changes in microclimate, nutrient cycling and runoff and erosion when forest is cleared and placed in pasture.

Microclimate

Light

Very little solar radiation penetrates to the floor of an evergreen or semi-deciduous tropical forest. The numerous strata in the forest each intercept a portion of the radiation until, on average, less than 10 percent of the original radiation reaches the floor (Snedaker, 1970). Snedaker (1970) also mentions that in a virgin forest in Guatemala only 4 percent of the solar radiation reached the soil surface. In a lowland rain forest in Malaysia the relative illuminance at ground level was only 0.29 percent (Yoda, 1974). Again, in a semi-evergreen seasonal forest in Thailand relative illuminance at ground level was 1.2 percent during the wet season and 1.7 percent during the dry season (Yoda et al., 1983).

How quickly light attenuates in a tropical forest depends on the vertical structure of the forest. In the same Malaysian lowland rain forest mentioned above, attenuation of solar radiation was correlated to leaf area index (LAI). The portions of the light profile with the highest LAI also had the greatest light attenuation. In the canopy of the forest the solar radiation was attenuated over 70 percent (Yoda, 1974). The LAI of the canopy was 7.8 compared to the LAI of the undergrowth which was 0.23 (Kato et al., 1974). A different trend was seen in the semi-evergreen seasonal forest in Thailand studied by Yoda et al. (1983) and in an evergreen oak forest in Japan (Yoda, 1978). In both of these forests the attenuation of radiation was more gradual through the light profile than in the Malaysian example. Both of these forests had better developed strata lower in the canopy than did the Malaysian forest.

Pastures can have levels of solar radiation at the soil surface similar to those found in tropical forests. A mixed pasture of *Setaria sphacelata* var. *sericea* (a grass) and *Desmodium intortum* (a legume), in which the legume was dominant, had a relative illuminance at the soil surface of less than 5 percent. However, in a mixed pasture where the *Sertaria sphacelata* was dominant over the *Desmodium intortum* the relative illuminance at the surface was over 10 percent (Ludlow and Wilson, 1983). The increase in the relative illuminance of the grass dominated pasture was attributed to the more vertical presentation of the grass leaves, which allowed more light penetration to the soil surface. This example illustrates that the structure and presentation of the plants in a pasture often results in a greater penetration of light to the soil surface than in closed forests.

Differences in relative illuminance in tropical forests and pasture can result in differences in light quality at the soil surface. Leaves absorb radiation primarily from the blue and red portions of the visible spectrum, while reflecting or transmitting light in the green and near infrared portions of the spectrum. Therefore the spectrum of light beneath a plant canopy is modified relative to the spectrum of light striking the canopy. Forests with low illuminances at the soil surface transmit a larger component of green and infrared light than forests with higher illuminances. Because pastures in general have higher illuminances at the soil surface than the typical tropical forest the pastures will have more blue and red light than a tropical forest. This difference in light spectra in the two systems impacts a wide variety of functions in plants. The actual amount of energy available to the plant for photosynthesis can vary. Regulatory functions are also impacted. The stimuli of elongation by blue light and of germination by the ratio of red and far red light are influenced when the light spectrum changes between forest and pasture. The role of light quality in germination will be discussed in a later section.

Temperature

Temperature profiles of forests and pastures differ considerably. These differences impact the temperature regimes of the soils under these plant communities. As discussed in the previous section, solar radiation impinges upon the upper surface of the canopy and is quickly attenuated as it passes through the upper parts of the canopy. The upper surface of the canopy is the "effective surface" for much of the exchange of energy that occurs in the forest

system (Larcher, 1980). Some of the solar radiation that strikes the effective surface is chemically converted by photosynthesis, reflected or transmitted. The rest of the radiation is absorbed by the leaf surfaces and degraded to infrared energy. This energy heats the surface of the leaves and causes this surface to have the highest temperature during the daytime of any part of the temperature profile. Aoki et al. (1975) found that the temperature of the canopy surface of a tropical rain forest in Malaysia was approximately 6 ° C higher than any other point in the temperature profile at the time of day with the highest temperature. In the temperate zone a similar trend occurs. The tree tops of a spruce forest in midsummer had a mean daytime temperature of 21.6 ° C while within the closed canopy the mean temperature was 21.1 ° C (Baumgartner as cited in Geiger, 1961). The rest of the temperature profile was cooler still.

The daily range of temperatures at the surface of the forest canopy is the greatest of any part of the profile. A forest in Malaysia had a mean daily range of temperatures at the canopy surface of 10.4 ° C (Aoki et al., 1975), while a spruce forest had a daily range at tree top of 19.4 ° C (Baumgartner as cited in Geiger, 1961). The temperature range decreases as one moves down the profile until the minimum temperature range is found at the soil surface. The Malaysian forest discussed above had a temperature range of 1.9 ° C at the soil surface and the spruce forest from above had a surface temperature range of 14 ° C.

In an evergreen tropical forest there is very little seasonal change in the temperature beneath the canopy. The continuous crown closure maintains near constant temperatures. However, in a semi-deciduous tropical forest the temperature beneath the canopy varies as crown closure changes throughout the

year. In a Costa Rican dry forest, Daubenmire (1972) found that during the wet season, when the canopy was fully intact, that the temperature under the canopy at the a height of 50 centimeters above the ground averaged around 30 ° C. When there was partial opening of the canopy during the dry season the temperature under the canopy approached an average of 40 ° C. Soil temperatures in this forest climbed about 4 ° C during the dry season.

The "effective surface" of a pasture is different then that of a forest. The near vertical display of leaves by the grass component of the pasture results in a more gradual drop in relative illuminance through the canopy than occurs in a forest. This results in a more gradual change in the temperature descending through the canopy. Also, because more light generally reaches the soil surface in a pasture than in a forest, the maximum temperature at the soil surface is higher than in a forest. However, there are numerous exceptions to this general statement. Pastures with large components of non-grass herbaceous plants have lower relative illuminances and therefore lower temperatures at the soil surface than do grass dominated pastures. Also, pastures that are grazed heavily have lesser crown closure than lightly grazed pastures and will transmit more light to the surface. Higher surface temperatures are the result.

The litter layer of a pasture can play an important role in determining the temperature of the soil surface. In an ungrazed pasture the litter layer builds as grass tops die back. A large part of the litter layer is compased of still air spaces which inhibit conduction of heat. The litter layer insulates the soil surface from the extremes in temperature above the litter layer. The soil surface consequently remains cooler than the region above the litter layer. The inability of the litter layer to conduct heat well also means that the surface of the litter

layer can become very warm. A litter layer composed of small conifer needles can have a surface temperature as high a 75 ° C when exposed to full sunlight (Smith, 1986).

When a pasture is grazed leaf material is consumed by the grazer instead of senescing and becoming part of the litter layer. The litter layer, as a consequence, is reduced as grazing increases. When there is a corresponding decrease in crown closure associated with the grazing, the increased relative illumination at the soil surface increases the temperature of the soil during the daytime. During the night the lack of insulation from the litter layer can result in a reduction in the surface temperature of the soil because of increased radiation and convection.

Soil temperatures during the day will be, on the whole, higher in pasture soils than in forest soils. The increased relative illumination at the soil surface in grazed pastures is the cause of this increase.

Moisture

The following discussion will examine factors that influence the presence of water in both the evergreen and the semi-deciduous tropical forest. The factors will be examined at several locations in the system, under the canopy, in the surface soil and deeper in the soil. The soil profile is divided on the basis of the different mechanisms at work. The water regime of a pasture also will be examined in a similar fashion. The impact of differences in grazing pressure on water allocation in the pasture system will be discussed as well.

There are several forces working in any plant community to influence moisture distribution. They are inputs to the system in the form of precipitation, overland flow or subsurface flow and outputs in the form of runoff, internal soil drainage, evaporation and transpiration. The energy potentials that drive the flows of these inputs or outputs come from solar radiation, gravity or the interaction of charged surfaces with the bipolar water molecule.

Rain falling on a tropical forest encounters resistance to its fall first in the canopy. Much of the intercepted rain eventually reaches the surface, however, the residence time of the water in the canopy can be quite long. Rain hitting the canopy can take several pathways to the ground. Rain that hits leaves will normally run off and continue falling to the ground. However, rain that hits the branches and stems of the trees will take longer to reach the ground, if it reaches it at all. Some of the stem flow is caught in pockets within the branches of the trees where it sustains epiphytes and canopy dwelling animals. The rest of the stem flow becomes concentrated as it flows to the ground down the stem of the tree. Some rain never reaches the surface but rather directly evaporates. Greenland and Kowal (1960) found in Ghana that 16 percent of the rainfall intercepted by a forest canopy evaporated.

The rain that reaches the ground beneath the forest canopy can either evaporate, run off or infiltrate into the soil. The low relative illuminance at ground level in an evergreen tropical forest provides little energy to evaporate water, so little water is lost by that pathway. The well established litter layer in an undisturbed forest retards movement of water through runoff so little water is lost in this pathway. The remaining water infiltrates into the soil.

Soil water interacts with the atmosphere in two basic ways, through evaporation or transpiration. Evaporation takes place at the soil surface or, when the soil is covered, in the litter layer. However, the depth to which water can be drawn by evaporation is very limited. As water evaporates from the soil or litter surface capillary action draws water from lower in the soil. However, the matric potential of the near surface soil becomes greater as water is drawn from ever smaller pores. Also, the gravitational potential increases as water is drawn from an ever increasing depth. These two potentials soon become great enough to prevent the continued loss of soil water. Seldom is water drawn more than a few centimeters by evaporation (Smith,1986).

As was mentioned above, the low level of solar radiation that reaches the ground in an evergreen tropical forest precludes any great loss of soil water by evaporation. The surface of the ground under this type of forest stays relatively moist. In a semi-deciduous tropical forest the opening of the canopy during the dry season results in a much greater drying of the forest floor relative to the evergreen tropical forest.

In the moist tropical forest, transpiration is the major pathway of water movement from the soil to the atmosphere. From one-half to two-thirds of precipitation is lost through transpiration (Keller, 1961). The roots of trees in the forest may extend to great depths and extract water from the soil. Roots also proliferate near the surface or just beneath the litter layer in forests where the litter layer acts as an effective mulch. In semi-deciduous forests the litter layer and upper level of soil can dry enough that roots in this zone are ephemeral, only growing into this zone during the rainy season.

The same mechanisms of water transport function in pasture as in forest. However, the relative importance of the mechanisms is not the same. Runoff in a pasture normally exceeds that from a forest. Greater amounts of rain reach the ground in pastures because the canopy of the pasture is less than that in the forest and less rainfall is intercepted and evaporated. Also, livestock grazing increases runoff. As the grazing pressure increases the level of vegetative cover decreases. The effectiveness of the vegetative cover in slowing runoff decreases as well. Therefore less water is available for infiltration. The infiltration rate of the soil of pastures is also frequently less than that in forests. Livestock treading causes compaction of the soil, which inhibits downward movement of water into the soil (Brooks et al., 1991).

The greater relative illuminance at the surface in a pasture compared to a forest results in a greater loss of water in the upper level of the soil to evaporation. However, the amount of evaporation is greatly impacted by the composition of the vegetative cover of the pasture. Pastures dominated by herbs or legumes will have less evaporation from the surface because of the greater leaf area index when compared to grass dominated pastures. Also, any pasture that is ungrazed or lightly grazed will have a greater leaf area index than a more heavily grazed pasture and therefore will lose less water through evaporation (Humphreys, 1991).

Transpiration in tropical pastures is also less than in a tropical forest. The grasses that predominate the improved pastures have significantly less root mass than forests and the roots do not reach as deep (Klinge and Herrera, 1978; Taerum, 1970; Jones, 1980). In tropical regions with no dry season, forest soils tend to be drier than pasture soils. The dryness also occurs at greater depths.

However, in regions with distinct dry seasons the opposite occurs. During the rainy season the forest transpires at a greater rate than a pasture and the soil profile tends to dry more quickly if there are any short dry spells. However, when the dry season begins many of the trees in the forest become dormant and no longer transpire at any great rate. The overall transpiration rate of the forest declines and the soil dries less rapidly than during the rainy season. The grazed grasses and forbs in the pasture do not become dormant on the basis of the photoperiod as do the forest trees and continue to transpire until soil moisture becomes short. The effect of this difference between the pasture plants and the forest plants is that the soil in the pasture becomes much drier to a greater depth than in the forest. Daubenmire (1972) observed this phenomenon in Costa Rica where the soil moisture in a soil profile in a *Hyparrhenis rufa* pasture to a depth of one meter was below the wilting coefficient for three months during the dry season. The soil in a nearby forest was below the wilting coefficient only to a depth of 20 centimeters during the same period.

An overall comparison of forest and pasture water movement indicates that runoff in pastures, in general, tends to be greater than in forests, especially as grazing intensity increases. Evaporation of water from the upper portion of the soil profile also tends to be higher in pastures than in forests because of the greater amount of solar radiation reaching the surface. Again, evaporation increases as grazing intensity increases. However, transpiration is greater in forests than in pastures in areas with weak or nonexistent dry seasons because of the greater root mass and leaf surface area in the forest. In areas with pronounced dry seasons the photoperiod induced dormancy of many of the forest trees reduce transpiration losses during the dry season compared to the

transpiration in the pasture, where the grazed grasses and forbs only become dormant later in the dry season as reduced soil moisture produces moisture stress.

Nutrient cycling

It would appear intuitive that conversion of a tropical moist forest to pasture would have a large impact on soil characteristics. When a forest is cleared there are profound changes in the pools of biomass and nutrients, as well as large changes in the microclimate of the sites. Studies, primarily related with clearing of tropical forest for cropping, have shown dramatic increases in ambient and soil temperatures and lower relative humidity and infiltration rates when forests are converted to cropland (Lal and Cummings,1979). The elevated soil temperatures cause an increase in the rate of decomposition of organic matter. For every 10 ° C increase in temperature, within the range of growth, there is a doubling of microbial activity (Paul and Clark, 1989). Lower relative humidity can increase the rate of evapotranspiration thereby lowering the moisture content of the surface layer of soil and decreased infiltration reduces the amount of water entering the soil.

Numerous studies have documented the large losses of carbon and nutrients that occur when forest is converted to agricultural uses. Burning the felled slash liberates large amounts of carbon and nutrients that are lost from the system by volatization, runoff or leaching. The pasture that follows has much smaller pools of organic carbon and nitrogen in the above ground biomass, below ground biomass and the litter layer. Uhl and Jordan (1984) found that the

primary forest they studied in the upper Rio Negro region of the Amazon Basin had above-ground biomass of 260,965 kg ha^{-1}, fine litter and dead wood had 28,850 kg ha^{-1} and roots had 48,525 kg ha^{-1} of biomass. These totaled 338,340 kg ha^{-1}. Compared to that, they found that a 5-year-old successional forest derived from pasture had a total biomass of only 122,382 kg ha^{-1}. Soil N under the primary forest was 1,722 kg ha^{-1} versus 741 kg ha^{-1} for the successional forest.

In research directly studying pastures, Yadava and Kakati (1985) reported that pastures in northeastern India dominated by *Bothriochloa intermedia* and *Imperata cylindrica* had a yearly above-ground net primary production of 15,680 kg ha^{-1}, below-ground net primary production of 8,950 kg ha^{-1} and total dead biomass of 14,420 kg ha^{-1}. The total biomass in the system was 39,050 kg ha^{-1}. In Colombia, a *Hyparrhenia rufa* pasture with a six-week cutting regime and with 50 kg ha^{-1} of nitrogen applied after each cut had an annual net above-ground biomass production of 4,500 kg ha^{-1} (Crowder et al., 1970). These examples of biomass production and accumulation illustrate the increased production and accumulation of biomass in a forest compared to a pasture.

On the basis of rates of biomass production and accumulation one might predict that soil organic carbon levels and nitrogen levels would be lower in the pasture than in the forest. However, this is not always the case. Buschbacher et al. (1988) found that soil nutrient stocks of nitrogen in abandoned pastures were comparable to the soil stocks of nitrogen under primary forest (about 7,000 kg ha^{-1} for both). This was despite the fact that the total site nutrient stocks of nitrogen (which included soil nitrogen stocks plus nitrogen stocks in the biomass and litter) in the primary forest were much higher than in the abandoned

pastures (about 10,000 kg ha^{-1} for primary forest versus about 7,600 kg ha^{-1} for abandoned pasture).

The similar levels of soil organic carbon and total nitrogen in forest and pasture can be explained by examining an equation for calculating soil organic matter accumulation and observing how the values of the variables of the equation change when comparing organic matter accumulation in forest and pasture. Sanchez (1976) used an equation dealing with the addition and decomposition of organic matter to discuss the equilibrium of organic matter in the soil. The equation is:

Equation 1: $$C=\frac{bm}{k}$$

where C = soil organic carbon at equilibrium (tons ha^{-1})

b = the annual amount of fresh organic matter added to the soil (tons ha^{-1} per year)

m = the amount of fresh organic matter converted into soil organic carbon (percent)

k = the annual amount of soil organic carbon lost through respiration (percent per year)

The annual addition of organic matter to the soil (b) includes estimates of the contribution from litter, branches and dead roots. For a pasture it also includes additions of organic matter to the soil from manure. Estimates of organic matter addition that include contributions from all sources are difficult to find. Sanchez (1976) has estimates of (b) for tropical forests that range from 3.85 tons ha^{-1} per year for a forest in Colombia with a udic soil moisture regime,

to 6.05 tons ha^{-1} per year for tropical forest in Zaire also with a udic soil moisture regime. These values include contributions from all sources. Estimates of soil organic matter additions for tropical savannas in Ghana are also given. They range from 0.44 tons ha^{-1} per year for an area with 850 mm of rain to 1.43 tons ha^{-1} per year for an area with 1250 mm of rain. Jordan (1983) gives estimates of litter production only for tropical forests ranging from 2.1 tons ha^{-1} per year for a tropical rain forest in the Ivory Coast, to 23.2 tons ha^{-1} per year for a rain forest in Thailand. Lamotte and Bourliére (1983) give litter production for savannas in Kenya ranging from 1.1 tons ha^{-1} per year to 2.3 tons ha^{-1} per year. As can be seen from these figures, even though the ranges of additions of organic matter vary considerably, there is a clear indication that tropical forests have larger additions than tropical grasslands. Therefore, if the conversion of fresh organic matter into soil organic carbon (m) and the decomposition rate of soil organic carbon (k) were the same for tropical forest and tropical grasslands then the forest would have significantly higher equilibrium levels of soil organic carbon.

In the case of m, tropical forests and grasslands are similar. Greenland and Nye (1959) show values of m ranging from 37 percent for temperate prairie to 51 percent for tropical forest. The value of m varies more between climates than between different plant communities in the same climate. For both tropical forest and tropical grasslands the values of m are similar.

However k is not the same for forests and grasslands. Tropical forests with similar climates as grasslands tend to have higher rates of k than the grasslands. Several micro-climatic factors control the rate of k. Temperatures of the soil and the litter are very important. There is a doubling of microbial

activity in soil (within the appropriate range of temperatures) for every 10°C increase in the temperature (Paul and Clark, 1989). Herrera de Fournier and Fournier (1977) found that a pasture in the Puriscal region of Costa Rica had an average soil temperature of 29.3°C while a nearby 30-year-old secondary forest had an average soil temperature of 22.3°C. This 7°C increase in temperature should almost double the rate of k in the pasture. However, the overriding microclimatic factor influencing k appears to be moisture levels in the litter. Sanchez (1976) related that k in a tropical forest in Ghana with an ustic soil moisture regime was 2.5% while a tropical savanna in Ghana with a similar soil moisture regime had a k of only 1.2% per annum. The difference is due to the increased litter moisture in the shaded understory of the tropical forest.

The increased additions of organic matter b in a tropical forest compared to the additions in a tropical savanna are associated with increased k in the tropical forest. This situation can result in combinations of b and k that produce similar levels of soil organic carbon in the tropical forest as in the tropical grassland.

Since the levels of total nitrogen in soil are closely tied to the levels of soil organic matter, similar levels of soil organic matter in forests and pastures can easily lead to similar levels of total nitrogen as well.

Carbon Cycling

The carbon cycling of a tropical pasture is much different than the cycling which occurs in a tropical forest. Even though the two systems share many of the same pathways the rates of movement in various pathways are different and

the importance of the pathways also differ. Figure 1 is a generalized schematic of the carbon cycling which could apply to either a tropical pasture ecosystem or to a tropical forest ecosystem. Both ecosystems have the same living carbon pools of plants, herbivores and decomposers and the same non-living carbon pools of litter, excreta and the atmosphere.

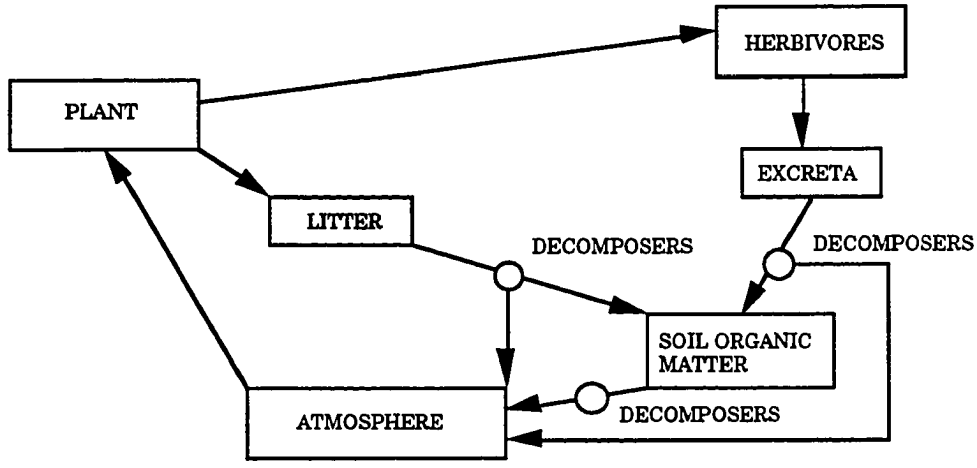

Figure 1. Generalized schematic of pools and pathways for carbon cycling within a plant community. The pools and pathways associated with the carnivores of the community are not shown for the sake of simplicity.

However, there are great differences in the sizes of the carbon pools and flux rates between the two ecosystems. The tropical forest has a large carbon pool in the standing biomass while the tropical pasture has a relatively small standing biomass pool. Litter levels in the tropical forest are also quite high compared to the tropical pasture, though the rate of decomposition of the litter in

the forest is much faster than in the pasture for reasons discussed in an earlier section.

The key difference between the tropical forest carbon cycle and the tropical pasture cycle lies in the larger role herbivores play in the cycling of carbon in the pasture. In a study of two grassland types in the Serengeti, Sinclair (1983) found that between 28% and 38% of the above-ground grass production was removed by herbivores per year, while the remaining grass production ends up in the litter pool after senescence. Typically only 5% to 10% of the above-ground biomass in a tropical forest are removed by herbivores per year (Odum, 1970; Jordan, 1983).

The shifting of carbon from the litter pathway to the herbivore pathway can greatly impact the amount of carbon that accumulates in the soil. The rate of movement of carbon through the herbivore pathway is often faster than the movement of carbon through the litter pathway because the C:N ratio of excreta of herbivores is narrower than the C:N ratio of most litter (Humphreys, 1978). The narrower C:N ratio of the excreta results in it being decomposed more quickly than the litter. If no other mechanism slows the rate of decomposition, it would be expected that tropical pasture soils would have higher soil organic carbon contents than tropical forest soils in similar climatic and edaphic conditions.

The apparent conflict between the hypothesis that forest and pasture soils can have similar levels of carbon and nitrogen discussed in an earlier section and the one proposed above can be rectified by examining the annual amount of fresh organic matter added to the soil or (*b*). The rate of movement of carbon through the herbivore and litter pathways corresponds to (*b*). The evidence for similar

soil organic carbon levels in forests and pastures would suggest that in those situations the quicker movement of carbon through the herbivore pathway is offset by other mechanisms that slow the rate of movement of carbon into the soil and result in a lower level of accumulation in the soil. Possible mechanisms are loss of nitrogen from the excreta through leaching or volatilization which widens the C:N ratio and slows the rate of decomposition, spatial redistribution of the excreta by the herbivores which causes a localized reduction in the amount of carbon available for decomposition, higher soil moisture tension in the pasture compared to the forest which limits the microbial action on the carbon in the excreta (Paul and Clark, 1989), and loss of soil organic carbon through erosion.

Nitrogen Cycling

The cycling of nitrogen through a tropical forest or a tropical pasture is very similar to the cycling of carbon in that many of the pools and pathways in the two ecosystems are similar (see Figure 2). However there are three ways nitrogen cycling differs from carbon cycling. These three ways act by impacting the litter and herbivore pathways. First, nitrogen is mobile within a plant and can be translocated from leaves, stems and other plant parts to other parts of the plant before senescence. The resulting litter has a lower level of nitrogen than if the nitrogen were relatively immobile like carbon. Second, when grass is harvested by an herbivore the entire amount of nitrogen in the grass is ingested by the herbivore and is not translocated out of the affected plant part. The translocation of nitrogen out of senescing plant parts and the retention of

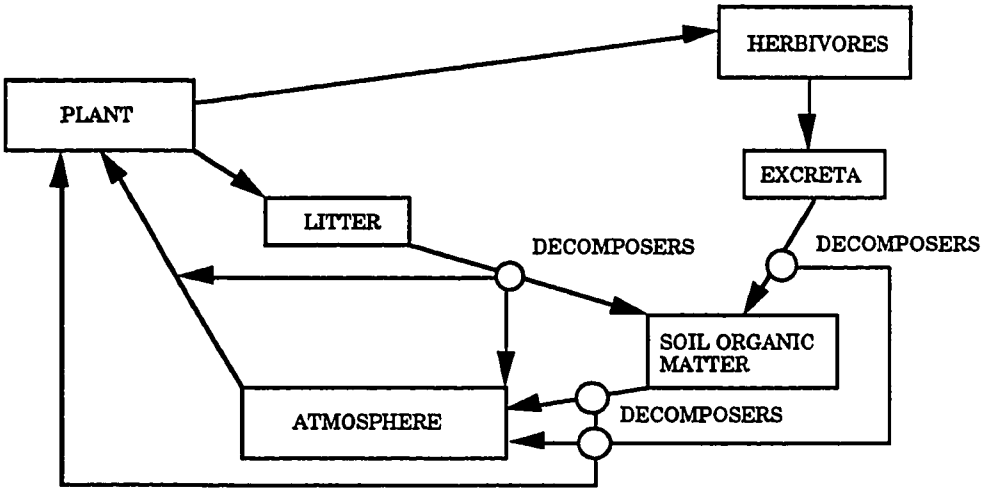

Figure 2. Generalized schematic of pools and pathways for nitrogen cycling within a plant community. The pools and pathways for the carnivores in the community are not included for the sake of simplicity.

nitrogen in browsed plant parts means that the herbivore pathway has a much higher potential for moving nitrogen into the soil than the litter pathway.

The third way in which nitrogen cycling differs from carbon cycling is that there is a large loss of nitrogen in the excreta of the herbivore prior to decomposition by volatilization of the urea in the urine. Vallis et al. (1985) indicated that in Australia 34% of the nitrogen in urine applied to a pasture in the dry season was lost to volatilizaton. This pathway of loss would tend to limit the rate of nitrogen movement through the herbivore pathway.

Even with the three differences between nitrogen cycling and carbon cycling discussed above, there are conditions that can lead to a greater accumulation of nitrogen in pasture soil than in forest soil. Rouquette, Matocha and Duble (1973) found that there was an increase in soil nitrogen levels as

stocking rate (SR) increased from 3 animals ha^{-1} to about 5 animals ha^{-1}. The increase in nitrogen occurred because at higher stocking rates more nitrogen was removed from the leaves by the cattle than at lower stocking rates. The nitrogen moved through the herbivore pathway instead of being translocated into ungrazed portions of the grass. By analogy, a forest, which has lower herbivory than a pasture, could also have lower total soil nitrogen than a pasture because the nitrogen is tied up longer in the standing and litter biomass.

Runoff and erosion

There are distinct differences in runoff and erosion between tropical forests and pastures. These differences are attributable to differences in vegetative cover and litter layers, in soil porosity and in root masses in areas susceptible to mass movement. Each of these differences will be discussed below.

Tropical forests and grazed pastures show significant differences in the levels of erosion. Undisturbed forest typically has very low levels of erosion compared to pasture. In the steep-sloped Arenal River catchment in Costa Rica, the average erosion in undisturbed forest was estimated at 1.4 tons ha^{-1} yr^{-1} (Holdridge and Tosi, 1973 as cited in Hartshorn et al., 1982). Improved pasture in the same watershed eroded at an estimated 109 tons ha^{-1} yr^{-1}. Forest in the Phewa Tal catchment in Nepal eroded at 8 tons ha^{-1} yr^{-1} while grazing land eroded at 34.7 tons ha^{-1} yr^{-1}. These erosion rates were for steep land.

The vegetative cover and the litter layer have much to do with the dynamics of erosion and explain much of the difference in erosion between

forests and pastures. The undisturbed forest has a continuous cover of vegetation which reduces the total amount of precipitation that falls to the forest floor. As mentioned before, Greenland and Kowal (1960) found that 16 percent of the precipitation falling on a forest in Ghana was evaporated from the canopy and therefore did not reach the forest floor. The litter layer in most tropical forests is also continuous. The litter layer shields the soil beneath from the kinetic energy of the falling raindrops. The litter prevents the detachment of soil particles by the splashing drops. The destructive force in falling rain drops is illustrated by results of an experiment done by Hudson (1957). Plots of bare soil were covered by two layers of wire gauze and the erosion rates of the plots were compared to adjacent bare soil plots without wire gauze. The average erosion rate for the protected plots was 1.02 tons ha^{-1} yr^{-1}, while the unprotected plots eroded an average of 119 tons ha^{-1} yr^{-1}.

The vegetative cover and the litter layer also protect pastures from erosion, but generally not to the same extent. Vegetative cover is often less in pastures than in undisturbed forest. Grazing livestock remove the vegetative cover to some extent and also impact the amount of plant material that is converted into litter. As grazing pressure increases the vegetative cover and litter layer provide less protection. In a study done by Eng et al. (1978) the amount of bare ground increased as stocking rates increased. Five percent of the pasture was bare with the lowest stocking rate of 2 cattle ha^{-1}. At a stocking rate of 6 cattle ha^{-1} bare ground increased to 30 percent. The impacts of reduced vegetative cover and a reduced litter layer were not separated in this study.

Pastures also tend to have higher runoff and lower infiltration rates than undisturbed forests. Several factors are involved. First, the bare surface can

become sealed when soil aggregates breakdown. The slaking and entrapment of air when the aggregates are quickly wetted can disrupt the aggregates (Cernuda, Smith and Vicente-Chandler, 1954). The soil pores near the surface can then become filled with soil particles reducing the infiltration rate. Second, infiltration rates can be reduced by compaction. The static and dynamic loads placed on soil by livestock during times of optimum soil moisture levels compresses the near-surface soil and reduces the proportion of large pores. Infiltration through the reduced pore space is greatly reduced because of the greater matric potential in the smaller pores. Daubenmire (1972) found that infiltration rates in a pasture in Guanacaste, Costa Rica were 47 times less than in an adjacent undisturbed forest.

The dynamics of runoff and erosion for "steeplands" (lands with slopes greater than 20 percent) is more complicated than for flatter lands. Several mechanisms come into play on the steeplands that are not active on flatter lands. First, mass movement becomes active. Mass movement is the transfer of slope-forming materials down slope *en masse* by the action of gravity. For example, this can occur as debris flows, slumping of soil blocks and slides. Mass movement is triggered by increases in the shear stress of the slope material and decreases in the shear strength. Common examples of factors that increase shear stress are earthquakes, increases in the mass of materials by infiltration of rain and greater loading of materials by the transient added weight of livestock. A common factor decreasing shear strength also involves water. Increases in soil water pore pressures can act like a lubricant and reduce the shear strength of material (Ritter,1986).

Deforestation increases mass movement (Lal, 1990; Hartshorn et al., 1982). In Nepal, it was found that mass movement increased 26 percent when an area was deforested (Laban, 1979 as cited in Lal, 1990). This author has seen pastures in the Puriscal region of Costa Rica which have had a greater proportion of their area in landslides than adjacent secondary forests. Mechanical reinforcement of the soil mass by the roots of trees is greater than the reinforcement from the roots of annual crops and pasture grasses (Lal, 1990). Not only is there more mass movement, in general, in pastures than in forests, but there also is more potential for mass movement in heavily grazed pastures than in lightly grazed ones. The more heavily grazed pasture has a greater load from livestock than the lightly grazed pasture. Therefore the shear stress is greater. Also, the shear strength of the soil material is reduced. The root mass of a heavily grazed pasture is less than the root mass in a lightly grazed pasture of the same forage species (Humphreys, 1991).

Runoff and erosion on steeplands is further complicated by the formation of grazing steps on these lands. Once slopes reach about 30 percent livestock choose to traverse across slopes rather than up or down slopes (Howard and Higgins, 1986). Livestock traversing slopes during periods of high soil moisture can quickly deform the hillside into a series of grazing steps perpendicular to the slope. Sheep grazing on an embankment in California created well defined grazing steps in only 6 weeks (Higgins, 1982).

Spacing between grazing steps is related to stocking rate. In California, a negative relationship was found to exist between stocking rate and spacing (Howard and Higgins, 1986). The spacing between the steps diminished as stocking rate increased. The cause was thought to be the need of the livestock to

create more steps to more fully utilize the pasture as stocking rates increased. The distance between steps stopped decreasing once the pasture was fully utilized.

Runoff and erosion are modified by grazing steps. Runoff and erosion are increased on the bare, compacted treads of the steps. The grazing steps can also act as terraces and pond water. The slower runoff results in greater infiltration. However, this slowing of runoff only occurs when the step treads slope towards the hillside. In overgrazed pastures the treads are eroded and slope in the same direction as the slope of the hill (Howard and Higgins, 1986). Runoff is not impeded by these grazing steps.

Operational Factors, Soil Characteristics and Tree Regeneration

The success of tree regeneration is dependent upon two circumstances. First, there must be a propagule available in a particular microsite before regeneration can proceed. Whether in the form of a seed or a sprout the propagule must be present. The second circumstance is that environmental conditions must be suitable for germination of a seed and its development into a seedling. In this study only seed germination will be examined. The environmental conditions (operational factors) suitable for seed germination are partially controlled by the soil characteristics of the seed bed. A link can be made between the operational factors involved in tree regeneration and the soil characteristics that influence the process.

A further link can be made between the operational factors that control tree regeneration and the site-quality assessment model developed by Gutiérrez

(1991). Operational factors (synecological coordinates) can be calculated from the physiognomic characteristics of a site using the model. Differences in tree regeneration success for undisturbed tropical forests and pastures can be indirectly observed by examining the differences in the synecological coordinates for the forests and the pastures. The concern of Costa Rican researchers that abandoned "degraded" pastures have delayed germination can be indirectly tested by examining the operational factors that control germination and the differences between these operational factors in undisturbed forests and pastures. Also, changes in the operational factors between pastures with different levels of "degradation" can be investigated to discover potential germination problems.

The following sections discuss the linkages between operational factors, soil characteristics and tree regeneration.

Operational factors

Every plant is surrounded by two environments (atmosphere and soil). Some portions of the environment directly influence a plant while others do not. If the environment is defined as the entire universe surrounding the plant then there are an infinite number of events and fluxes occurring in the universe that do not directly impact the plant. However, there also are a number of fluxes of energy and matter that do directly influence the plant and move from the atmosphere and soil through the surface of the plant into its interior. These fluxes of energy and matter, as a whole, make up the "operational environment" and individually can be called "operational factors" (Spomer, 1973).

There are a large number of energy and mass operational factors that influence a plant, such as radiation of various wavelengths (ionizing, light, thermal, etc.), mechanical energy, gases, liquids, solids, nutrients, hormones and toxins (Spomer, 1973). In this review only a few of the more important factors will be discussed. These include the energy factors of light and heat and the mass factors of water (liquids) and nutrients.

A number of non-operational factors that are normally considered as impacting a plant do so only indirectly. Such factors as temperature and water potential, among others, indirectly influence the plant by providing the driving forces that move operational factors into or out of the plant. For example, temperature gradients move heat across plant boundaries. A number of soil characteristics also indirectly impact operational factors. The next section discusses how these indirect soil characteristics influence operational factors.

Soil characteristics and operational factors

Light (radiation)

Soil characteristics impact the operational factor of light by modifying the light environment above and below the soil surface. The mode of modification is through reflection of light from the soil surface. While vegetation itself has a major impact on the light environment, bare soil and the litter layer (if it can be considered part of the soil surface) do contribute as well.

The reflectivity of the soil is dependent on its color and moisture. Color is the spectral variation in radiation as influenced by the temperature of a light

source or the reflective, absorptive and transmittive properties of materials (Lillesand and Kiefer, 1979). The color of soil (including the litter layer) is dependent on its mineralogy, its texture, its moisture content and the organic matter in or above the soil.

Smith (1986) submits that the amount of light reflected by most soil or organic matter is similar. Even charcoal, as black as it, reflects almost as much light as bare soil or litter. However, Lillesand and Kiefer (1979) discuss how soil characteristics greatly influence reflectance. The texture of a soil is important because particles of different sizes reflect different wavelengths of light. Also, water content influences reflectance. Moist soil reflects less light than dry soil.

Regardless of whether light reflectance varies between soils of differing characteristics or not, the overall amount of light reflected from any of these surfaces can be a significant portion of the solar radiation impinging on a plant. Over 20 percent of the light striking dry bare soil is reflected (Swain and Davis, 1978 as adapted by Lillesand and Kiefer, 1979). In most ecosystems there is little bare ground so light reflecting from it is of little importance, however, in some situations, such as after a forest fire, light reflected from bare ground can be a relatively large component of the light striking any plant becoming established. In pastures, the amount of light reflected from bare ground can increase with an increase in stocking rate. Eng et al. (1978) found that bare ground averaged 5, 10 and 30% respectively at stocking rates of 2, 4 and 6 cattle ha^{-1}.

Heat

Soil characteristics play an important role in the energy budget of the soil and the near-surface atmosphere. During the day, the heat content of soil increases as it absorbs solar radiation. During the night, soil cools as heat is radiated to the atmosphere. The first soil component that impacts the absorption of radiation during the day is the reflectivity of the surface. The previous section on light discussed the impact of soil characteristics on reflectivity. The radiation that is not reflected is absorbed by the soil and is converted into heat energy.

The heat flux into and out of the soil is controlled by conduction, convection and the specific heat and latent heat of vaporization of water. The heat energy absorbed by bare soil moves downward at a rate dependent on the thermal conductivity of the soil. The thermal conductivity of the soil, as a whole, is controlled by the thermal properties of the solid, liquid and gaseous phases. The heat capacity for these three constituents of the soil are, on average, 0.46 cal $cm^{-3} \circ C^{-1}$ for the mineral portion of the solid phase, 0.60 cal $cm^{-3} \circ C^{-1}$ for the organic portion, 1 cal $cm^{-3} \circ C^{-1}$ for water and for air the heat capacity is negligible (de Vries, 1963).

The water content of soil impacts greatly on its thermal conductivity. Nakshabandi and Kohnke (1965) showed that the thermal conductivity of wet sand was about 12 times greater than dry sand. Lesser increases were found for loam and clay, in that order, though wet clay still had a thermal conductivity almost 6 times that of dry clay. The greater thermal conductivity of wet soil allows quicker transport of heat into the soil, where it is stored. However, the

greater thermal conductivity does not necessarily translate into higher soil temperatures. The high specific heat of water means that large quantities of heat can be stored without an increase in temperature.

Soil texture also affects thermal conductivity. As the size of soil particles decreases, surface contact between the particles is reduced as well. Heat flow between particles is thus reduced (Jury et al., 1991). Increases in bulk density, as can occur with compaction, reverse the impact of soil particle size on flow of heat between particles by packing them closer together. In a study by van Rooyen and Winterkorn (1959) the thermal conductivity of a soil increased as the bulk density increased from 1.1 g cm^{-3} to 1.5 g cm^{-3}, especially when the fraction of pores filled with water exceeded 50 percent. Thermal conductivity at the highest bulk density of 1.5 g cm^{-3} almost doubled over the lowest bulk density of 1.1 g cm^{-3} with over 70 percent of the pores filled with water.

The latent heat of vaporization of water can move significant amounts of heat into and out of soil. Solar radiation striking a soil with a wet surface evaporates the water and delays the movement of heat into the soil. Convective air currents then transport this heat away from the surface. This phenomenon can be relatively short lived though. In the case of a soaked litter layer at noon, the evaporation of water in the litter may delay heating of the litter as little as one-half hour (Smith, 1986).

The presence of a litter layer over bare soil modifies the movement of heat into and out of the soil because the large amount of air entrapped in the pores of the litter limits the conduction of heat through the layer. The thermal conductivity of litter is about as low as any naturally occurring substance

(Smith, 1986). Heat movement in litter is so effectively slowed that temperatures at its upper surface can reach 75 ° C in direct sun (Smith, 1986).

Water (liquids)

The role of water in heat transport has been briefly discussed in the previous section. However, water plays other roles as well. Water is involved in the movement of nutrients within the soil and into and through plants. It also is essential for the survival of plants. Several soil characteristics control the availability of water in the soil. They are the particle size distribution of the soil and the structure. If the litter layer can be considered as part of the soil, it too plays a role in water loss and gain by the soil.

The litter layer influences water relations in the soil by protecting the soil from the impact of raindrops and thereby preventing sealing of the surface, by slowing runoff and increasing infiltration and by slowing evaporation of moisture from the soil surface. The role of litter in slowing evaporation and in protecting the soil surface from sealing have already been discussed in previous sections and will not be dealt with further here.

The litter layer slows runoff by obstructing the free movement of water from a slope. The impact of a litter layer can be quite dramatic. In a Litchi plantation in Taiwan, runoff accounted for 54 percent of the precipitation in the control treatment with no mulch, while runoff was reduced to 17 percent of precipitation for the "with mulch" treatment (Liao and Wu, 1987 as cited in Lal, 1990). In Peru, similar results were found in a comparison of the runoff from a corn-cowpea-potato rotation with and without mulch (Alegre et al., 1987 as cited

in Lal, 1990). The runoff from the rotation without mulch was 149 mm, while the runoff from the mulched rotation was 34 mm.

Litter can also increase infiltration rates. The increase can be attributed simply to delaying runoff long enough for the water to infiltrate the soil, or it can result from an actual increase in the infiltration rate of the soil. As organic material in the litter layer decays and is incorporated into the soil, the bulk density of the surface soil can decrease over what it would have been with just bare soil. Lal (1990) reported an increase in the saturated hydraulic conductivity of the 0 to 10 cm layer in soil for a wide variety of mulches. Increases of up to 28 fold over bare soil were reported.

Once water enters the soil, pore size distribution and structure control its retention and movement. A soil moisture characteristic curve (which relates water content changes to changes in water potential) readily shows the differences in water holding capacities of soils with different textures. Clay soils, with a large proportion of small pores, retains more water at higher tensions than sandy soils, which have a large proportion of large pores.

Structure has a complicated impact on water retention. Clay soils with well developed structure have more large pores than similar soils with poorly developed structure and consequently have slightly lower water holding capacities but better infiltration rates. Sandy soils, however, with well developed structure have better water holding capacities than unstructured sands because the organic matter which aids in the development of structure also has a higher water holding capacity than the sand.

Nutrients

Availability of nutrients to plants depends first on nutrients entering the soil. There are several routes. Nutrients can enter the soil from weathering of parent material, from dryfall or wetfall bringing nutrients in from the atmosphere, from fixation of atmospheric nitrogen by plants and microorganisms and from being imported into the site from outside sources (nutrients from imported manure or fertilizer).

Nutrients also can leave a soil by leaching, denitrification of nitrogen or by being exported from a soil when crops are harvested.

Several soil characteristics impact retention of nutrients in soils and also influence uptake by plants. They are the number of exchange sites that are available on clay minerals and humus, immobilization of nutrients in organic matter and the pH of the soil. The number of exchange sites in a soil is dependent not only on the amount of clay and humus in the soil, but also on the mineralogy of the clay. Different types of clay minerals have widely varying abilities to retain nutrients. The clay mineral kaolinite has a cation exchange capacity (CEC) in the range of 3 - 15 meq 100 g^{-1} dry weight. However, the clay mineral, smectite, has a CEC in the range of 80 - 150 meq 100 g^{-1} dry weight. The smectite has a much larger number of exchange sites for cations than does the kaolinite. Organic matter has even a higher CEC than smectite. The CEC of organic matter ranges from 150 - 500 meq 100 g^{-1} dry weight (Grim, 1968). Obviously, a soil high in organic matter (for example, a peat soil) would be capable of retaining more cations than would a soil high in smectite or kaolinite.

Nutrients can also be retained in the soil when immobilized in living organisms and dead organic matter. Nutrients can be taken up by organisms from the soil solution or by the consumption of other organisms. The nutrients are then bound up in the organic matter until the material is freed during mineralization.

The pH of soil determines the availability of a number of nutrients for uptake by plants. Nutrient availability changes with pH as the chemical forms of nutrients vary. For example, at pHs below 6 phosphorus can interact with iron and aluminum to form insoluble compounds that are unavailable for uptake by plants (Barber, 1984).

Operational factors, soil characteristics and tree regeneration

It is clear from the discussions in the previous sections that soil characteristics play an important role in determining the level of operational factors that influence plants. Operational factors impact the functioning of plants at all points in their life cycle, however, for the purposes of this study the impact of operational factors on plant life will be focused on tree germination.

Water

Imbibition of water by the nondormant seed is a precursor to the chain of events that leads to germination. All of the activities of the embryo are reactivated once sufficient water has been imbibed by the seed. The amount of water needed to promote germination is small and is usually not more than two

to three times the weight of the seed (Koller, 1972). The water necessary to start germination can be easily imbibed at low soil water potentials. However, increasing negative water potentials quickly reduce the rate of germination of seeds. Kaufmann (1969) found that water deficits of -230 kPa to -470 kPa were sufficient to hinder germination of citrus seeds. Germination of eucalypt seeds was very sensitive to soil matric potential. The germination rate fell rapidly from about 80 percent at a potential of 0 to around 30 percent at a potential of -5 kPa (Bachelard, 1985). As matric potential dropped further the germination rate continued to decline, but at a slower rate.

Any soil characteristics that influence water potential impact the germination rate of seeds. Particle size distribution, structure and the presence or absence of a litter layer all affect water potential. These soil characteristics have been discussed already in an earlier section. However, the influence of the litter layer on germination needs further discussion.

The poor heat holding capability of litter causes it to be a poor seedbed. As mentioned before, very high surface temperatures can occur when litter is exposed to direct solar radiation because of its low heat conductivity. Temperatures as high as 75 ° C are possible (Smith, 1986). The high temperature has a direct and an indirect impact on germination. The direct effect is the high temperature. Pitch pine (*Pinus rigida*) will germinate at temperatures as high as 57 ° C, but only rarely (USDA Forest Service, 1948). Seeds that land on a litter layer can easily be killed by the high temperatures. An indirect effect of high litter layer temperatures is the quick drying of the litter layer. Smith (1986) notes that a moist litter layer can dry in as little as one-half hour in the direct sun. While the litter layer makes a very poor

seedbed, bare soil is much better. The chances that a seed will germinate increase with the lower water potentials and lower temperatures associated with bare soil.

The water potential of the soil also can affect germination by influencing the amount of oxygen available for seed respiration. The amount of oxygen in the soil falls quickly in saturated conditions. Diffusion of oxygen in water is much slower than in air. When a soil becomes saturated with water, aerobic respiration from plants and microorganisms soon removes the oxygen from the water. Respiration at that point can then only continue along anaerobic pathways. Seeds are obligate aerobes and cannot tolerate anaerobic conditions for very longer before dying. However, the levels of tolerance does vary. Crawford (1977) found that the germination rate for *Oryza* spp. seeds submerged for three days was about 95 percent, while the germination rate of *Pisum* spp. seeds was almost 0 percent for the same period of submersion.

Any soil qualities that lead to saturated conditions will profoundly influence the oxygen status of the soil and the germination rate of any seeds. In moderately to well drained soils this condition only occurs with heavy, sustained precipitation, but if soils are compacted, periods of saturation near or at the surface can become more frequent and have a greater impact on germination.

Heat

The heat flux crossing between the boundary of the seed coat and its operational environment controls the internal heat content of the seed and affects germination. However, research on the effect of heat on germination has

focused on temperature, not on heat flux. Though heat is the operational factor, temperature gradients are the driving forces that transport heat into or out of a seed. Therefore, this section will deal with the effects of temperature on germination.

All seeds have a temperature range in which germination is optimal. However, some germination can usually take place over a broad temperature range. Many temperate-zone conifers can germinate in a broad range from about 4 - 10 ° C to an upper range of 35 - 40 ° C (Larcher, 1980). The optimum range of temperatures is 15 - 25 ° C. The C_4 grasses of the tropics can germinate over a range varying from a low of 10 - 20 ° C to a high of 45 - 50 ° C, though the optimum temperature range is a very narrow 32 - 40 ° C (Larcher, 1980).

Soil characteristics that affect germination through temperature are those that control heat movement into and out of the soil. They are particle size distribution and structure (as far as those characteristics influence water holding capacity and the associated movement of heat by conduction), the color of the soil and the presence of a litter layer. How these qualities modify heat content and temperatures has been discussed in previous sections.

Light

Light influences germination in three ways. Intensity of light has moderate impact on the germination of some seeds, while the duration of light and the wavelength play important roles. Only some seeds require light to germinate; many seeds will germinate in darkness as well as in light. Red pine

(*Pinus resinosa*), jack pine (*Pinus banksiana*) and eucalypts (*Eucalyptus* spp.) germinate equally well in light or dark (Heit, 1958; Heit, 1968).

For some tree species day length is important in stimulating germination. Most light-sensitive tree seeds respond most to day lengths of 8 to 12 hours (Kramer and Kozlowski, 1979).

Other tree seeds show changes in germination rates with variations in the wavelength of light, or more specifically, changes in the ratio of red to far red light (Hartman and Kester, 1983). Wavelength-sensitive seeds tend to be small and thus need to germinate near the surface in high levels of light to survive. The storage tissues are insufficient to fuel growth of deeply planted seeds for long enough for the seedlings to emerge from the ground. These seeds show higher germination rates when exposed to red light than to far red light. Virginia pine (*Pinus virginiana*) seed had a germination rate of 93 percent when exposed to red light, while seed exposed to far red light had a germination rate of about 4 percent (Toole et al., 1961). Red light is predominant in direct sunlight, while far red is dominant in shade conditions, such as in the understory of a forest.

Only two soil characteristics can modify the light operational factor for a seed (if the litter layer is included as part of the soil); the reflectivity of the surface and the shading caused by the litter layer. The reflection of light from bare soil or the litter layer would have little impact on modifying the light environment of the seed. While the red/ far red light ratio may change somewhat when light is reflected, the fact that perhaps only 20 percent of the incoming light is reflected would seem to indicate that the spectrum of the reflected light would be overpowered by the spectrum of the direct light.

Shading caused by the litter layer could influence the germination rates of light-sensitive seeds. Light intensities would be reduced and the red/ far red ratio might be modified by the transmission of light through the litter.

Nutrients

Nutrients do not play a role in seed germination (Smith, 1986). Rather, any nutrients needed by the germinating seed are taken from the storage tissues. It is only when the storage tissues become depleted and photosynthesis begins that nutrients begin to be extracted from the soil.

Summary

In Part II a site-quality assessment model is used to indirectly link changes in soil characteristics related to degradation with tree regeneration. In previous sections of this literature review an attempt has been made to link soil characteristics to operational factors of the environment and then to link operational factors with tree regeneration. The site-quality assessment model developed by Gutiérrez (1991) uses the method of synecological coordinates to quantify the operational factors of a site and then uses linear regression to link the operational factors to site physiognomic characteristics. The model can be used to predict the operational factors of a site. It is the contention of this author that those predicted operational factors indirectly say something about tree regeneration. The goal of the second part of the literature review was to establish that link.

Tree Regeneration Problems in Disturbed Sites of the Humid Tropics

Tree regeneration problems fall into two categories. The first category deals with shortfalls in operational factors that impede regeneration. The second category deals with problems caused by the lack of seed in the seed bank. Examples of the impact of the two categories on tree regeneration in the tropics will be discussed below.

Operational factors impeding regeneration

Very little research has been done in the tropics to quantify the impact of soil degradation on regeneration or to identify operational factors that may be limiting regeneration. However, some research has been done in several closely allied areas. A number of studies have examined the growth of tree seedlings on various types of degraded soils, though most of those studies did not look at what soil factors influenced growth. Other studies have explored how land clearing and pasturing modified secondary succession, but these studies, for the most part, did not attempt to identify how soil factors influenced succession, or else the role of soil factors was confounded with the role seed source had in the succession. However, several studies do give hints as to the impact of soil degradation on tree regeneration and those studies will be discussed below.

Uhl et al. (1982) studied the effects of three types of forest clearing on subsequent tree regeneration in southern Venezuela. The three treatments were cutting the forest, cutting plus burning and bulldozing alone. The sites were

abandoned after treatment and vegetation and soil characteristics were measured after three years. The results were that the cut site had abundant tree regeneration from sprouts and seed. The cut and burn site had abundant regeneration from seed, while the bulldozed site had almost no tree regeneration. The bulldozed site had substantially lower levels of every nutrient tested plus a very low amount of organic matter. The authors attributed the very poor regeneration to two causes. First, the only mode of regeneration available in the bulldozed treatment was seed dispersal. Sprouts and seeds in the seed bank were removed by the bulldozing. Regeneration could have been delayed on this site simply because it took time for seed to disperse into the site. Second, the authors attributed some of the delay to low soil fertility, though the responsible soil factors were not identified. As mentioned before, the level of fertility in the bulldozed site was very low compared to the other treatments, however, it was impossible to determine the impact of the soil fertility on tree regeneration because the effect was confounded with the effect of seed dispersal.

In a small study done in the United States Virgin Islands, Brown and Ray (1993) did not find any differences between the soil organic matter and nitrogen content of an abandoned pasture with poor regeneration and of several well stocked secondary forest sites. This project did not have replications of the treatments and therefore the results are somewhat suspect.

A few studies have looked at the impact of soil degradation on tree growth. Growth of *Cordia alliodora* on an oxisol in Surinam was reduced by two-thirds on a bulldozer-cleared site compared to a site cleared using slash and burn (van der Weert and Lenselink, 1973). In Brazil, the diameter at breast height (dbh) of cacao trees on land cleared by slash and burn was significantly higher than the

dbh of cacao trees on land cleared by bulldozing (Silva, 1982). Silva (1983) attributed the difference to lower infiltration rates, decreased exchangeable bases and decreased organic carbon on the site cleared by bulldozing. The differences were the result of the slash, the litter layer and the upper part of the soil being removed by the bulldozer.

Several studies in Costa Rica have examined tree regeneration in abandoned pastures, but none of the studies have identified any problems with regeneration. Two abandoned sites in the Puriscal region of Costa Rica, which are within the study area of this research, have been studied by Fournier and Herrera de Fournier (1985). They have found that secondary forest succession has proceeded quickly on both sites. One site, after nine years, had 26 of a possible 37 tree families represented on the site and that 52 out of a possible 103 tree species were represented on the site. The other site had 34 of 38 possible tree families present after 20 years and 84 of a possible 110 tree species. It appears that regeneration was not limited on these two sites. However, the extent of soil degradation (if any) on these sites is not known. The author has examined a small, nondegraded (as defined by the landowner) abandoned pasture near one of the sites discussed in Fournier and Herrera de Fournier (1985) one year after its abandonment. The vegetation consisted of grasses, lianas, shrubs and trees up to two meters in height. Again, at this site regeneration did not appear to be impeded.

In eastern Costa Rica, Reiners et al. (1994) studied the effects of converting lowland tropical rain forest to pasture and subsequent succession of pasture land to secondary forest. They found that pastures abandoned 4 to 10 years had total organic carbon levels in the soil similar to active pastures and

lower than secondary or primary forest. The abandoned pastures also had total nitrogen levels lower than the other three land uses. In spite of the low fertility of the soils in the abandoned pastures, the number of tree taxa on the sites was comparable to the numbers found in the secondary and primary forest sites. In this case, the lower fertility in the abandoned pastures was not sufficient to hinder tree regeneration.

Even though the studies mentioned above found no regeneration problems in abandoned pastures there is still a perception that some pastures in Costa Rica do not easily return to secondary forest when abandoned. Fournier (1990) and Solórzano et al. (1991) both suggest that that is the case. An ongoing study in the Rio Picagres watershed of Costa Rica may be demonstrating the delay of germination of forest tree seeds in abandoned pastures, however, no causal agent has yet been found (Gutiérrez, 1994, personal communications).

Seed factors impeding regeneration

In a series of articles dealing with secondary forest succession in northeast Brazil Buschbacher et al. (1988), and Nepstad et al. (1990) found that soil conditions in abandoned pastures were not an impediment to regeneration. The most degraded pastures did have delayed regeneration, but that was attributed to a shortage of tree propagules. The length of time since clearing was long enough that there were no longer any sprouts arising from relict roots. The seed bank predominately contained seeds from annuals, grasses and forbs (Uhl and Clark, 1983). Studies in other locations have found similar results (Guevara S. and Gómez-Pompa, 1972; Kellman, 1974). Trees were poorly represented in the

seed bank because of shortfalls in the mechanisms of tree seed dispersal into the pastures. There were two reasons for the poor dispersal. First, large tree seeds, which would have had the highest probability of survival in a pasture, were not carried into the pastures. The birds, bats and ground animals which would normally disperse the large seeds tend to avoid the open spaces in pastures. The tree seeds most likely to arrive in pastures were wind dispersed seeds. However, these seeds have low probabilities of survival because of seed predation.

Summary

Problems with tree regeneration fall into two categories; impediments caused by limiting operational factors or impediments caused by a limited seed source. The preceding section discussed a number of studies that related to both of these categories. Of the studies that examined the impact of land use change on regeneration success, very few focused on identifying operational factors that might be limiting regeneration. Several studies looked at the influence of different land clearing techniques on subsequent tree regeneration. Clearing of forest with bulldozers did limit regeneration success but it was unclear whether the poor regeneration was due to soil degradation or limited seed sources.

A few studies examined the influence of forest clearing and fire on tree growth. Reduced growth was attributed to lower infiltration rates, decreased exchangeable bases and organic carbon. Unfortuntely these studies did not look at regeneration.

A number of studies in Costa Rica looked at the influence of land use changes and associated changes in soil characteristics on tree regeneration.

None of these studies found a link between soil fertility and regeneration. However, anecdotal information infers that in the Puriscal region of Costa Rica there may be a tree regeneration problem on some pasture sites. It is clear that additional studies need to be conducted to identify if there is indeed a regeneration problem and if there is, what operational factors are causing the problem.

The study in Part II attempts to indirectly determine if soil operational factors are limiting tree regeneration in pastures in the Puriscal region of Costa Rica. A site-quality assessment model will be used to relate changes in soil characteristics to changes in the suitability of the pastures for regeneration of several tropical tree species.

Literature Review Summary

The preceding literature review was in three parts. The first part reviewed literature concerning forest clearing and grazing and the impact of both on microclimate, nutrient cycling, runoff and erosion. Forest clearing typically occurs in two forms; clearing for shifting agriculture and potentially permanent clearing for other land uses. The potentially permanent clearing has by far the most impact on soil characteristics. The microclimate in sites cleared for semi-permanent land uses changes drastically, with an increase in solar radiation which leads to increased temperatures in the near surface atmosphere and in the soil. There are also changes in the runoff and infiltration of rainfall and resulting changes in erosion.

Clearing a forest and converting it to pasture causes significant changes in nutrient cycling. The change in microclimate, plus changes in the types of plants cause changes in the amount of organic matter that entires the soil each year and in the amount of carbon that is lost through respiration. Amazingly, in a particular climate, reduction of the amount of organic matter added to the soil in pastures is often offset by a reduction in respiration so that a tropical pasture ends up having a similar amount of soil organic carbon at equilibrium as a tropical forest.

Introducing herbivores into a pasture system has a big influence on nutrient cycling. Without herbivores, the nutrients in plant tops are either recycled by being translocated into other parts of the plant or are cycled back to the plant through the litter. The tops of the plant die and become litter. The litter is then consumed by soil organisms and part of it becomes soil organic matter. The nutrients in the soil organic matter are eventually mineralized and taken up by plants. When herbivores are introduced much of the above ground biomass is consumed by the animals instead of becoming litter. The nutrients moving through the herbivores cycle more quickly and can accumulate to higher levels in the soil than if the herbivores were not present.

The second part of the literature review looked at the operational factors of the environment (water, heat, radiation, oxygen and nutrients) that influence trees. These operational factors pass between the air and soil into the tree and influence its entire life cycle. Soil characteristics greatly influence the operational factors not only in the soil but also in the atmosphere near the soil surface. Soil characteristics influence how solar radiation impacts plants, how

heat is transferred to the plant, how much water is available to the plant and what quantity of nutrients will be available to the plant.

Operational factors of the environment also influence tree seed germination. The amount of water, quantity of heat and the quantity and quality of light available to a seed play a role in the germination of that seed. Nutrients do not influence germination, because the seed carries its own source of nutrients.

The last part of the literature review examined studies done in the tropics relating to tree regeneration and soil degradation. Few studies specifically examined pasture degradation. Some studies looked at tree regeneration after land clearing and some studies examined the influence of soil degradation on tree growth. Several studies in Costa Rica examined tree regeneration in abandoned pastures, but found no link between tree regeneration and soil degradation. The most infertile pastures, in these studies, had abundant regeneration.

There is still a perception that in the Puriscal region of Costa Rica that there are tree regeneration problems in some abandoned pastures. The next two parts discuss two studies that were conducted to attempt to answer whether there are problems with tree regeneration in this part of Costa Rica. The first study examines the soils of undisturbed forests and compares them with adjacent pastures. The second study uses a site-quality-assessment model to indirectly examine the influence of soil characteristics on tree regeneration.

PART I.

A COMPARISON OF SOIL CHARACTERISTICS OF PASTURES AND PRIMARY FOREST IN THE TROPICAL MOIST PREMONTANE LIFE ZONE IN COSTA RICA

INTRODUCTION

A study was conducted in the Puriscal region of Costa Rica in 1993 which compared several soil characteristics in pasture plots with the soil characteristics in paired plots of undisturbed primary tropical moist forest. The study also examined soil characteristics in three erosion classes in pastures. The problem that this study addresses has been discussed in the general introduction and the literature review and will not be repeated here.

Two hypotheses were tested in the study. The first hypothesis is that clearing an undisturbed tropical moist forest and converting it to pasture will cause soil degradation as shown by reductions in the levels of organic carbon and total nitrogen, increases in bulk density and clay content, and a decrease in soil pH in the surface horizons of soils.

The second hypothesis is that soils can be classified by erosion groups that are related to soil degradation. Erosion group 1 (the least eroded) will have the least soil degradation as shown by it having lowest increase in bulk density and clay content and the lowest decrease in total nitrogen, pH and organic carbon. The other two groups will have changes in soil characteristics proportional to their defined level of erosion.

MATERIALS AND METHODS

Study Area

The study area was in the Tropical Moist Forest, Premontane Belt Transition Life Zone (Tosi, 1969) in the Puriscal region of Costa Rica about 30 km southwest of the capital, San José. The study area reaches from the town of San Ramón in the northwest to San Ignacio de Acosta in the southeast, a distance of approximately 50 km. The Life Zone in this area covers approximately 340 km^2. The area is mountainous with slopes as steep as 100%. Annual precipitation is greater than 2000 mm of rainfall with a distinct dry season from November to early May (Fournier y Herrera de Fournier, 1985). Even with the high precipitation the soil moisture regime is ustic. The mean temperature of the area is 23 ° C, with seasonal variation of less than 5° C. The bedrock of the region varies from volcanic breccia, lavas, and andesitic-basaltic intrusions to sedimentary rocks, such as sandstone and limestone. The soils in the area are primarily Lithic Ustropepts, Lithic Ustorthents, and Ustic Tropo Humults (Alvarado, Glover and Obando, 1982). The Canton of Mora, which is in the study area, has been extensively used for row-crop production and cattle grazing for several hundred years. The area was once a major producer of corn (*Zea mays*) and beans (*Phaseolus vulgaris*), but because of soil degradation land use shifted to pasture (Bolaños, 1983).

The primary forest in the Tropical Moist Forest, Premontane Belt Transition Life Zone is tall and has multiple strata. The forest has both semi-deciduous and evergreen tree species. The canopy trees are 40-50 m tall. Lianas

of large diameter are common, as are epiphytes. Tree ferns occur in the understory.

Plot Design and Layout

Sampling was done on paired plots. One plot was located in undisturbed primary forest and the other in an adjacent pasture. The paired plots were similar in slope angle, slope aspect, soil type and altitude. The plots were located in near proximity of each other (adjacent in many cases). Each plot consisted of two parallel transects separated by 5 meters. The transects were 50 meters long. Soil sample subplots were located every 5 meters along each transect. There were ten soil sample subplots per plot.

Preliminary plot selections were done using aerial photos for two dates: 1974 and 1989. Locations with fragments of potential primary forest with adjacent pasture were identified on the 1989 photos. The same areas were examined on the 1974 photos to see if the 1989 pasture plots had been in pasture at that time. Plots that had remained in pasture over the period were selected for examination on the ground. Ground surveys identified 24 paired plots that met the above criteria.

In several locations individual pastures were quite large (greater than 5 hectares). These pastures often had extensive interfaces with undisturbed primary forest. Several paired plots were located in each of these pastures. The paired plots were separated by a minimum of 130 meters. The broken, steep topography of the Puriscal region meant that none of these closely spaced paired plots were similar in topography and therefore they could be treated separately.

The physical characteristics and vegetation of each plot were recorded. The following information was recorded in each forest plot: the slope angle, slope aspect, slope position; canopy height, soil order (as determined by locating the plots on a soil map of the area (Vasquez, 1989)), approximate size of the forest fragment, number of vegetative strata, predominant understory plants, presence and abundance of epiphytes, presence and size of lianas (large diameter, slow growing lianas indicated a relatively old forest), presence of grasses, evidence of erosion (gullies, rills, mass movement) and signs of grazing and/or logging. On the pasture plots, the following information was collected: the slope angle, slope aspect, slope position, soil order (determined by locating plot on soil map of the area (Vasquez, 1989)), species of grass present, approximate size of the pasture, estimate of ground cover, evidence of erosion (gullies, rills, mass movement), presence and size of grazing steps, grass height, overall vigor of the pasture and the presence of livestock. The information from the forest plots was used to identify undisturbed primary forest. Information from both plots in each pair was used to assure paired plots were similar. The physical and vegetal data collected in the pasture plots were used to classify pasture plots into erosion groups.

In pasture plots with grazing steps, care was taken when laying out the sampling transects so that no bias would be introduced because of the regular spacing of the steps. In pasture plots that did not have grazing steps, the transects were perpendicular to the slope. However, if a pasture plot had grazing steps the transects were laid out diagonal to the slope to prevent the soil sampling subplots from falling completely within a grazing-step or in the riser between steps.

The forest plots were aligned perpendicular to the slope. However, if obstacles were encountered (trees, rocks) the plot layouts were modified to avoid the obstacles.

Soil samples were collected from the upper 15 cm of the soil at the ten subplots within each plot. The samples were bulked for testing in 20 of the paired plots. On four of the paired plots, the samples from the subplots were analyzed separately. The samples in these paired plots were kept separate so that within-plot variation could be measured.

Cores for bulk density were taken at each subplot using a corer with a diameter of 44 mm and a depth of 50 mm (Blake, 1965a). The cores were oven dried and weighed at the Centro de Investigaciones Agronomicas at the Universidad de Costa Rica. The 5 cm deep measurements of bulk density were converted to estimates of bulk density for the upper 15 cm of the soil so that the bulk density estimates could be used to calculate organic carbon and total nitrogen masses determined on 15 cm deep cores. The estimated bulk density for the upper 15 cm of the soil was calculated by multiplying the measured bulk density of the 0-5 cm deep core by a predetermined correction factor for each of the 5-10 cm and the 10-15 cm depths. The mean bulk density for 0-15 cm was then calculated by averaging the bulk densities of the three depths. The correction factors by which the two lower depths were multiplied were derived from bulk densities found for the same depths in a study done in eastern Costa Rica (Veldkamp, 1994). The correction factors for forest were 1.00 for the 0-5 cm depth, 1.10 for the 5-10 cm depth and 1.14 for the 10-15 cm depth. The percentages for pasture were 100% for the 0-5 cm depth, 114% for the 5-10 cm depth and 115% for the 10-15 depth.

Particle-size analysis was done using the Bouyoucos method (Day, 1965). Organic carbon was analyzed using the Walkley-Black procedure (Reeuwijk, 1987). Soil pH was measured with a pH meter in a 0.01 M solution of $CaCl_2$ (Kalra and Maynard, 1991). Air-dried samples were tested at the Iowa State University Department of Forestry for the presence of allophane (which binds with organic matter) using a field test developed by Fieldes and Perrott (1966). The total nitrogen determinations were done at the Iowa State University Department of Agronomy using the permanganate-reduced iron modified Kjeldahl method (Bremner and Mulvaney, 1982).

Organic carbon contents (C_S) for the paired plots were converted to total organic content (TOC) using the 0-15 cm soil layer thickness (L) and bulk density, (p_b). The concentration of organic carbon was transformed from a concentration to an amount per volume of soil using equation 2 (modified from Veldkamp, 1994).

Equation 2: $$TOC = C_S \, L \, p_b \times 10^5$$

Total nitrogen contents (N_S) for the paired plots were also converted to total nitrogen content per hectare (TN) using the 0-15 cm soil layer thickness (L), and bulk density, (p_b). The concentration of total nitrogen was transformed from a concentration to an amount per volume of soil using equation 3 (modified from Veldkamp, 1994).

Equation 3: $$TN = N_S \, L \, p_b \times 10^5$$

The organic carbon and total nitrogen concentrations were converted to amounts per volume because the total amount of a nutrient in a volume of soil is a better indication of the amount of nutrient available for nutrient cycling than the concentration of that nutrient.

Erosion Group Definitions

Pasture plots were classified by placing them into one of three erosion groups. The erosion groups were defined using modifications of definitions for erosion grades found in a land capability classification system developed by Tosi O. (1985a) for use in Costa Rica. Table 1 defines the three erosion groups, with erosion group 1 having the lowest amount of erosion and erosion group 3 having the highest level of erosion. The grades are qualitative definitions for erosion and are somewhat subject to individual interpretation. Also the boundaries between grades are somewhat blurred. However, even with these limitations it was relatively easy to classify the pasture plots. The grading system was used to classify the 24 pasture sites into 3 groups.

The erosion group definitions are manifestations of several forces at work in a pasture. These forces are the increase of bare areas by the action of livestock hooves or by the reduction of plant vigor from overgrazing (Humphreys, 1991), the creation of grazing steps as a result of the grazing habits of livestock (Howard and Higgins, 1987), and the increase in mass movement as a result of soil modification by compaction and the increased loading of the soil by the static and dynamic forces created by livestock (Humphreys, 1991).

Table 1. The definitions for the three erosion classes used for classifying the twenty-four pastures plots (modified from Tosi O., 1985)

Erosion Group	Definition
1	No signs of erosion or light marks of trampling in the pastures.
2	Shallow paths between grass clumps on slopes <27% or grazing steps with completely vegetated risers and no mass movement of soil blocks on slopes >27%.
3	Deep paths between grass clumps on slopes <27% or grazing steps with only partially vegetated risers or displacement of blocks of soil on slopes >27%.

The paths of bare soil between clumps of grass are manifestations of the decrease in ground cover resulting from the disturbance of soil by the hooves of livestock and the reduction in plant vigor as a result of overgrazing. The growth characteristics of the predominant plant in the pasture plots (the grass, *Hyparrhenia rufa*) vary as the intensity of grazing changes. Under light grazing and in the absence of burning, *H. rufa* takes on a bunch grass form, with bare ground between bunches of grass. Under heavier grazing, *H. rufa* changes to a stoloniferous growth pattern. The stoloniferous form covers the ground more completely than the bunch grass form. Hogaboom (1952) found in Honduras that the optimal stocking rate for maintaining the greatest level of ground cover was around one and one-quarter cattle ha^{-1}. This stocking rate will vary somewhat with site characteristics. Stocking rates in excess of the optimal cause

a decrease in ground cover. Therefore, there is a reduction in ground cover both when a pasture is undergrazed and when it is overgrazed. The overgrazed state can be differentiated from the undergrazed state by the absence of bunch grass in the overgrazed pasture.

The grazing habits of livestock often cause the formation of grazing steps on slopes steeper than about 27%. Cattle, in particular, have difficulty in moving up or down slopes greater than 27% and choose instead to concentrate their movements to paths across the slopes (Higgins, 1982). These movements during times of high soil moisture cause deformation of the soil into relatively flat terraces. This deformation occurs most noticeably on soils that are highly plastic when wet. The spacing of the steps is a function of the stocking rate. Howard and Higgins (1987) found that as stocking rate increases, up to a point, the spacing between grazing steps decreases. This is caused by a greater utilization of the pasture by the cattle at higher stocking rates. Once the optimal stocking rate has been reached, any further increases in stocking rate only cause degradation of the ground cover of the risers between the steps and does not cause a reduction in the spacing of the steps. It is the presence or partial loss of ground cover on the risers that is used to indicate the difference in degradation between erosion group 2 and erosion group 3.

A further criterion for differentiating between erosion group 2 and erosion group 3 is the presence or absence of mass movement of the soil. The steepness of slopes in the Puriscal area result in slope instability. Increased soil moisture at the beginning of the wet season, earthquakes and increased stocking rates (Humphreys, 1991) all increase shear stress on the slopes. Increased pore water pressure in the soil decreases shear strength. Both forces can greatly increase

the probability of mass movement. The mass movement mentioned in the erosion group definitions is related to the movement of soil blocks associated with the grazing steps. Increased stocking rates not only cause partial loss of vegetation on the risers but also can increase the loading on the steps and cause movement of the blocks. This phenomenon primarily occurs on the steeper slopes. The likelihood of mass movement increases as the slope steepens.

RESULTS

Site Descriptions

Field work for this study was conducted from mid-January to late March of 1993. A total of twenty-four paired plots were found to fit the criteria of undisturbed primary forest with an adjacent pasture with site characteristics (ie., slope angle, slope aspect, soil order, etc.) similar to the forest. It was very difficult to find appropriate sites because very little primary forest remains in this Life Zone. Seventy-four paired plots initially identified from aerial photos were examined on the ground and rejected. These plots were rejected for a number of reasons. In some rejected paired plots the forests were secondary instead of primary, in some there was evidence of grazing in the forests, and in some the forest and pasture were not comparable because the forest fragments were in gullies while the pastures were on adjacent flatter slopes.

Table 2 lists the characteristics of the paired plots and the number of paired plots in each category. The majority of the paired plots (18) were in the higher altitudes of the Life Zone (820 - 900 meters). The majority of paired plots (15) fell into the 26 - 60 % slope angle category. However, a sizable number of paired plots had slopes less than 25% (5), while two paired plots had slopes in excess of 70%. Most slopes (14) had north aspects. A majority of paired plots (15) were in a midslope slope position. Paired plots were somewhat evenly divided between Ultisols (13) and Alfisols (9). All of the pasture plots had *Hyparrhenia rufa* (jaragua grass) as the predominant species of grass. The raw

Table 2. A compilation of the site characteristics identified at the 24 paired forest and pasture plots

Site characteristic	Categories	Number of sites
Elevation	540-700m	6
	820-920m	18
Slope aspect	North	14
	East	4
	South	2
	West	4
Slope angle	0-25%	6
	26-60%	15
	61% +	3
Slope position	Shoulder	6
	Mid-slope	14
	Toe	4
Soil order	Ultisol	13
	Alfisol	11

data for the twenty extensively sampled paired plots and for the four intensively sampled paired plots are in Appendices 1 and 2, respectively.

Forest and Pasture Comparisons

Table 3 shows the means of the five soil characteristics for the forest and pasture plots. Paired t-tests were used to test the hypothesis of no significant differences between the soil characteristics of the forest and pasture plots. There were pronounced differences between forest and pasture plots for bulk density and for pH. The mean bulk density of the forest plots was significantly lower in the upper 15 cm of the soil than in the pasture plots. Also the forest plots had

Table 3. The means for bulk density, clay content, organic carbon, pH and total nitrogen of the 0-15 cm layer for the forest and pasture plots. All soil characteristics were tested to a P value of 0.05

Plot	Corrected bulk density (g cm^{-3})	Clay (%)	Total organic carbon (kg ha^{-1})	pH	Total nitrogen (kg ha^{-1})
Forest	0.89**	30.7	52,350	5.10**	4,925
Pasture	1.03**	31.9	52,630	4.79**	5,018
SE[1]	0.03	1.51	3,358	0.05	288
P-value[2]	0.0003	0.4463	0.9335	0.0001	0.7482

** significant at the 0.01 level

1 SE is the standard error of the difference between the forest and pasture plots from a paired t test

2 the P-value is the probability of a greater t value under the null hypothesis of no treatment differences

significantly higher pHs than the pasture plots. There seemed to be marked differences between forest and pasture plots for clay, total organic carbon or total nitrogen.

Erosion Group Comparisons

The least-square means of the soil characteristics of the three erosion groups were adjusted by using the associated forest means as covariates. This reduced variation is comparable to the reduction in variation that occurs with a paired t-test. The soil characteristics for the forest plot corresponding to the appropriate pasture plot were used as covariates. These least-square means

were tested for significant differences. Table 4 shows the results of that testing. The least-square mean bulk density and pH were not significantly different between the three groups. However, clay content, total organic carbon content and total nitrogen showed notable differences. The least-square mean clay content of erosion group 1 (28.3%) was not significantly different than that of erosion group 2 (33.7%), but was different than that of erosion group 3 (36.0%). Similarly, the clay content of erosion groups 2 and 3 were not significantly different from each other but they were different than erosion group 1.

The least-square means for total organic carbon were markedly different between the three groups. Erosion group 1 had the largest amount of total

Table 4. Comparison of the least-square means [1] of the soil characteristics of the 3 erosion groups for the 0-15 cm layer

Erosion Group	Corrected bulk density (g cm^{-3})	Clay content (%)	Organic carbon (kg ha^{-1})	pH	Total nitrogen (kg ha^{-1})
1	1.02 A[2]	28.3 A	65,930 A	4.8 A	6,115 A
SE[3]	0.03	2.09	3,297	0.07	280
n=11					
2	1.08 A	33.7 AB	50,420 B	4.8 A	4,752 B
SE	0.06	3.25	4,402	0.09	537
n=6					
3	0.99 A	36.0 B	37,520 C	4.8 A	4,083 B
SE	0.04	2.58	5,244	0.08	450
n=7					

1 least-square means are adjusted means using associated forest means as covariates

2 means with different letters are significantly different at the 0.05 level

3 SE is the standard error for each erosion group

organic carbon (65,930 kg ha^{-1}), erosion group 2 had the next largest (50,420 kg ha^{-1}) and erosion group 3 had the smallest amount of total organic carbon (37,520 kg ha^{-1}). The least-square mean for total nitrogen content for erosion group 1 (6,115 kg ha^{-1}) was significantly larger than the other groups (group 2: 4,752 kg ha^{-1} and group 3: 4,083 kg ha^{-1}) The least-square means for erosion groups 2 and 3 were not significantly different from each other.

Erosion Group and Forest Comparisons

The least-square means of each erosion group and the least-square means of the associated forests are in Table 5. The least-square means were tested for significant differences between the erosion group means and the means of the associated forest plots.

The mean corrected bulk density for erosion group 1 (1.05 g cm^{-3}) was notably higher than the mean bulk density for the associated forest (0.92 g cm^{-3}). There was no significant difference in clay content between erosion group 1 and the forest. Erosion group 1 had a markedly higher level of mean total organic carbon (60,930 kg ha^{-1}) than the mean total organic carbon for the associated forest (47,940 kg ha^{-1}). The mean pH for erosion group 1 (4.8) was significantly lower than the mean pH for the associated forest (5.1). The mean total nitrogen for erosion group 1 (6,008 kg ha^{-1}) was significantly higher than the mean total nitrogen of the associated forest (4,818 kg ha^{-1}).

The only soil characteristic mean that was significantly different between erosion group 2 and the associated forest was the corrected bulk density. The

Table 5. A comparison of the means of the soil characteristics of the three erosion groups and the means of the soil characteristics of the associated forest plots for the 0-15 cm layer

Plot	Corrected bulk density (g cm^{-3})	Clay content (%)	Organic carbon (kg ha^{-1})	pH	Total nitrogen (kg ha^{-1})
Forest n=11	0.92**	28.8	47,940**	5.1**	4,818**
Erosion Group 1	1.05**	26.6	60,930**	4.8**	6,008**
SE[1]/P[2]	0.03/0.0017	2.10/0.3235	3,405/0.0034	0.04/0.001	269/0.0013
Forest n=6	0.83**	36.3	48,700	5.1	4,267
Erosion Group 2	1.04**	38.0	47,490	4.7	3,992
SE/P	0.02/0.0002	2.14/0.4712	2,269/0.6166	0.16/0.572	146/0.1178
Forest n=7	0.89	28.9	62,400**	5.1	5,656*
Erosion Group 3	0.99	34.9	44,010**	4.8	4,343*
SE/P	0.10/0.5054	2.84/0.0795	3,672/0.0024	0.17/0.126	469/0.0310

* Signifies a significant difference between the forest and the erosion group at the 0.05 level

** Signifies a significant difference between the forest and the erosion group at the 0.01 level

1 SE is the standard error of the difference between each erosion group and its associated forest plots from a paired t test

2 the P-value is the probability of a greater t value under the null hypothesis of no treatment differences

mean corrected bulk density for erosion group 2 (1.04 g cm^{-3}) was significantly higher than the mean corrected bulk density for the associated forest (0.83 g cm^{-3}). There were no significant differences in the mean clay contents, total organic carbon, pH or total nitrogen between erosion group 2 and the associated forest.

The mean total organic carbon for erosion group 3 (44,010 kg ha^{-1}) was significantly lower than the mean total organic carbon for the associated forest (62,400 kg ha^{-1}). The mean total nitrogen for erosion group 3 (4,343 kg ha^{-1}) also was lower than for the associated forest (5,656 kg ha^{-1}). The means for the corrected bulk density, clay content and pH were not significantly different between erosion group 3 and the associated forest.

DISCUSSION

Forest and Pasture Comparisons

The first hypothesis of this field study was that clearing of tropical forest for pasture would cause soil degradation as measured by an increase in bulk density and clay content and a decrease in organic carbon, total nitrogen and pH in pasture soils. The following paragraphs will discuss how the results relate to this hypothesis.

It was hypothesized that the soil of a pasture would have a greater bulk density than a forest soil. The results agree with this. The bulk density of the pasture plots was greater than that of the forest plots. A possible cause of the increase is compaction of the soil through the action of livestock. A number of studies have shown this impact (Humphreys, 1991; Daubenmire, 1972; Taboada and Lavado, 1988). Another possible cause of the increased bulk density could be exposure of the higher bulk density textural B horizon because of erosion. The Bt horizon in many of the Alfisols and Ultisols in this region of Costa Rica are quite close to the surface, sometimes being as close as 15 cm (Alvarado et al., 1982). However, erosion is probably not the cause of the bulk density increase, as will be explained in the next paragraph.

An increase in clay content of the pasture soils over the forest soils was expected. It was expected that the pasture soils would be subjected to more erosion than the forest soils and that the higher clay Bt horizon might be exposed. However, there was no increase in clay content. There are two possible explanations. First, if there was greater leaching in the pasture soil there would

be greater translocation of clay out of the surface soil. In eastern Costa Rica, Wielemaker and Lansu (1985) found that in a matter of months after clearing a rain forest there was translocation of clay out of the surface soil. Translocation is probably not occurring in the pasture soils in this area because of differences in the rainfall amount and distribution from eastern Costa Rica. Eastern Costa Rica has much higher precipitation than the Puriscal region (4000 mm versus 2400 mm). There also is no dry season. The potential for leaching in eastern Costa Rica is much greater than in the Puriscal region. Another study shows that if there was any clay translocation in the soils in the study area it would likely occur in the forest soils. As was mentioned in the literature review, Daubenmire (1972) found in western Costa Rica that the changes in soil moisture throughout the year in pasture are much different than in forest. The soil in the pasture became much drier in the dry season than did the soil in the forest. Consequently there would be less leaching and clay translocation in the pasture than in the forest. The climate in the Puriscal area is more similar to the climate in Duabenmire's study area than it is to the climate in eastern Costa Rica.

It was hypothesized that there would be a decrease in organic carbon and total nitrogen contents in the pasture soils compared to the forest soils. This was not the case. Neither organic carbon or total nitrogen decreased. The reason for this lack of decline may be related to the soil organic carbon equilibrium model discussed in the literature review (Sanchez, 1976). A line of reasoning was followed in the literature review that said that even though pastures have lower inputs of organic carbon and nitrogen than tropical forests they also have lower amounts of organic carbon and nitrogen lost through

microbial respiration. The lower inputs of organic carbon and nitrogen in tropical pastures is offset by the lower microbial respiration and can result in pasture soils having levels of carbon and nitrogen similar to those found in forest soils.

The lower pH found in the pasture soils was expected, though the mechanism responsible for the decrease is not clear. Leaching often causes a loss of exchangeable bases and a decrease in pH, however, as was discussed above, potential for leaching in the pasture is probably less than in the forest. Loss of organic matter can also result in the loss of exchangeable bases, but that has not happened in this case. Forest and pasture organic carbon are similar. Bases also are be removed when cattle are harvested. However, these removals of nutrients and bases are fairly insignificant for beef cattle. Humphreys (1991) notes that a 500 kg live weight gain ha^{-1} yr^{-1} represents only 12, 4 and 1 kg ha^{-1} of N, P and K, respectively. It is unclear then, what mechanism is causing the lower pH in the pasture plots.

Erosion Group Comparisons

The hypothesis concerning the erosion groups stated that there would be an increase in soil degradation moving from the least eroded soils to the most eroded soils, as shown by an increase in bulk density and clay content and a decrease in organic carbon, pH and total nitrogen in the more eroded soils. The results of the field study will be tested against this hypothesis.

There were no significant differences in the bulk density of the three erosion groups. This was not expected. It was expected that the higher stocking

rate often associated with increased erosion would cause greater compaction of the soil in the more eroded groups. The lack of change in the bulk density may be explained by an interaction of compaction of the soil by livestock and the loosening of the soil resulting from mass movement. It was apparent in many of the more steeply-sloped pasture plots that the treads of the grazing steps were very compacted from the high traffic on the steps. However, this compaction may have been offset somewhat if the grazing steps slipped (as was often the case in erosion group 3). The movement of the steps mixed the soil at the plane of weakness and the ripping of grass roots separated peds. The bulk density in these zones was quite low. The lower bulk density in areas of mass movement may have offset the higher bulk density in the treads and resulted in no overall increase in bulk density.

There was an increase in clay content in the more eroded groups. The clay content of erosion group 3 plots was significantly higher than erosion group 1 plots. This agrees with the hypothesis. A probable cause is the exposure of the clay-rich Bt horizon by erosion. While the clay content of all of the pasture plots did not increase over the forest plots, it appears that the above average erosion in erosion group 3 could lead to the Bt horizon being exposed.

The decrease in total organic carbon and total nitrogen as the plots became more eroded was expected. It is likely that the organic matter-rich surface layer of the soil has been removed from the more eroded plots. This would occur at a greater rate for the more highly eroded group 3.

The lack of change in the pH between the erosion groups is difficult to explain. It would be expected that the pH of the soil would be less on the more eroded plots because of exposure of the subsoil and loss of organic carbon and

nitrogen. The pH of soils in this region typically declines with depth (Alvarado, 1982). The pH results would seem to indicate that erosion was not greater in erosion groups 2 and 3. However, this goes against the evidence provided for erosion by the increase in clay and the decrease of organic carbon and nitrogen in the more eroded groups. The mechanism responsible for the pH decline is unclear.

Erosion Group and Forest Comparisons

A comparison of the erosion groups with their associated forest plots is a great aid in identifying possible reasons for the changes (or lack of changes) in soil characteristics between forest and pasture plots and between erosion groups. Comparing erosion groups with forest plots passes the data through a finer toothed comb by combining an examination of the changes between forest and pasture plots with an examination of changes between erosion groups. The changes will be discussed in the following paragraphs. The section will be organized by soil characteristic, rather than by erosion group so that the mechanisms influencing the soil characteristics can be more easily compared across erosion groups.

Bulk density

The bulk densities for erosion groups 1 and 2 were higher than that in the associated forest plots. This was expected. The likely reason for the increase, as discussed before, is the compaction of the erosion group soil by livestock.

The lack of significant difference between the bulk density in erosion group 3 and the associated forest plots was unexpected. A possible explanation is that there was an actual increase in bulk density from the associated forest plots to erosion group 3, but the increase was not statistically significant because of the high standard error for the six plots in the erosion group. The mean bulk density for erosion group 3 was 0.99 g cm^{-3}, while the average bulk density for the associated forest plots was 0.89 g cm^{-3}. The standard error for the comparison of erosion group and forest was 0.10 g cm^{-3}. This standard error was three times higher than the standard errors of the comparisons for either erosion group 1 and 2. The increased variability in erosion group 3 may be a result of the definition used to classify plots into this group. Defining erosion group 3 plots on the basis of depth of paths between grass slopes or the displacement of soil blocks combines, in one definition, two mechanisms that have very different impacts on bulk density. The part of the definition dealing with the depth of paths focuses on the impact of the loading of livestock on compaction of the soil. The displacement of soil blocks focuses on the role of livestock loading on the loosening of soil along the stress planes of the blocks. These two mechanisms have opposite effects on compaction and may account for the high variability in bulk density between plots.

Clay content

The lack of significant change in the clay content of the erosion group soils was not anticipated. The lack of difference in erosion group 1 was expected because the implied low erosion levels would seem to indicate that clay content

would not be different than in the forest plots because little of the surface of the soil in the erosion group would have been lost and therefore the Bt horizon would not have been exposed. However an increase in clay content was predicted as the levels of erosion increased in erosion groups 2 and 3. Perhaps the erosion, even in erosion group 3, has not been severe enough to expose the Bt horizon yet.

Total organic carbon and total nitrogen

The increases in total organic carbon and total nitrogen in erosion group 1 were totally unexpected. There are two possible explanations for the increase. First, part or all of the increase may be caused by the compaction of the soils in this erosion group. If two equally thick soil layers initially had similar levels of carbon and nitrogen, compaction of one of the soils would cause an increase in amount of carbon and nitrogen per unit volume. To compare the carbon and nitrogen levels in these soils properly it would be necessary to compensate for the reduced thickness of the layer that had been compacted. Veldkamp (1994) uses this technique to compare uncompacted forest soils with compacted pasture soils. However, in this study it was not possible to compensate for the compaction. There were two reasons for this. The first reason was that the corresponding layers in the forest and pasture plots were not identified. Rather the soil was sampled to uniform depth. Sampling this way meant that the compacted pasture soil layer corresponding to a layer in the forest plot was sampled along with a layer of soil beneath that layer. Compensation for the compaction could not be done because the two samples did not represent the same initial profile. The second reason for not compensating for compaction was

because the process does not take into account loss of soil by erosion. Any loss of soil from the top of a soil layer would change the layer so it could not be compared to a layer that was initially similar.

A second possible explanation for the increase in carbon and nitrogen in erosion group 1 is that the grazing of the pasture may have increased the rate of nutrient cycling. This concept relates to changes in the pathways of nutrient cycling when herbivores are integrated into a system. Carbon and nitrogen are cycled more quickly through the "herbivore" than through the "litter" pathway in a pasture. Carbon and nitrogen levels in the soil may increase when this occurs. Overall, carbon and nitrogen quantities in the entire soil, plant, animal system may decreased compared to the forest due to greater microbial respiration, etc., but more of the remaining carbon and nitrogen may be concentrated in the soil. A more in-depth discussion of this idea can be found in the literature review.

It was anticipated that the total organic carbon and total nitrogen amounts in erosion group 2 would be less than for the associated forest plots. This was not the case. The amounts were similar. The lack of difference in the amounts can not be attributed to the impact of compaction as discussed earlier because if compaction played a role in the amounts present in the erosion group the group would have had significantly larger amounts of carbon and nitrogen than the forest plots. This would occur because the erosion group had a significantly higher bulk density than the forest plots.

The lack of differences may be caused by two opposing mechanisms. First, increased nutrient cycling through the "herbivore" pathway may be working to increase the amounts of organic carbon and total nitrogen, while increased

erosion may be working to decrease the amounts by removing the organic carbon and total nitrogen from the plots. The two forces may cancel each other out.

The decreased total organic carbon and total nitrogen amounts in erosion group 3, compared to the associated forest plots, may be caused by the work of one force, erosion. The increased erosion in the erosion group would remove the carbon and the nitrogen from the surface layer of the soil.

The impact of pH

The decrease in pH in erosion group 1 was similar to the decline observed in the analysis of all of the forest and pasture plots. Again, the mechanism operating in this situation is not clear. Leaching of the exchangeable bases does not seem to be a plausible explanation because of the lower leaching in pastures, compared to forests. Decrease in the exchangeable bases through loss of organic matter by way of erosion also does not seem to work as an explanation because of the low erosion in this group.

The lack of difference in the pH for erosion groups 2 and 3 would seem to agree with the supposition that pastures would have lower leaching than forests in this region. But would disagree with the idea that erosion reduces pH by removing organic matter from the surface layer of the soil. By definition, the level of erosion should increase from erosion group 2 to group 3 and there should be a similar increase in the removal of organic matter, as was the case in erosion group 3. The mechanism at work here is unclear.

CONCLUSION

A study was conducted in the Puriscal region of Costa Rica to identify soil degradation in pastures. Physiognomic data were collected from twenty-four combined plots of undisturbed forest and pasture. Soil samples were analyzed for measurements of bulk density, soil particle distribution, organic carbon, pH and total nitrogen. A comparison of all forest plots with all pasture plots found significant differences in bulk density and pH. Bulk density was greater in the pasture plots than in the forest plots and pH was lower in the pasture plots. The increased bulk density in the pasture was attributed to soil compaction from the treading of livestock. The lower pH was attributed to a decrease in exchangeable bases, though the mechanism involved was not clear.

A comparison of three pasture erosion groups found increasing clay contents as erosion increased and decreasing amounts of total organic carbon and total nitrogen as erosion increased. The increasing clay and decreasing carbon and nitrogen were attributed to the loss of the surface layer of the soil through erosion.

A comparison of erosion groups with their associated forest plots found several unusual trends. For erosion group 1, there was an increase in bulk density compared to the forest plots, a decrease in pH and, most unusually, an increase in the amount of total organic carbon and total nitrogen from the forest plots to the erosion group. The increased bulk density was ascribed to increased compaction from livestock, the pH decrease could not be explained by the actions of leaching or erosion and the increase in carbon and nitrogen was thought to be caused by an increased concentration of carbon and nitrogen in the pasture

because of compaction or by an increased cycling of the nutrients through the "herbivore" pathway. The two factors could not be separated because of the sampling technique used in this study.

This study has raised as many questions as it has answered. Examining how the definitions of the erosion groups relate to actual erosion might help reduce experimental error in studies, such as this one, and would help better illuminate the factors controlling the changes in soil characteristics between erosion groups. It would certainly be worthwhile to study the role grazing has in modifying nutrient cycling in pastures. That would help explain the increases in carbon and nitrogen found in erosion group 1.

It would be useful to determine how compaction and erosion influence the size of nutrient pools in the pasture soils. As it now stands in the study, the effects of the two factors are confounded. It also would be helpful to identify the mechanisms impacting clay contents and pH levels. Several results tended to disagree with conventional hypotheses about factors controlling clay contents and pH levels.

PART II.

A SITE-QUALITY MODEL FOR ASSESSING TREE REGENERATION SUCCESS IN PASTURES IN THE TROPICAL MOIST PREMONTANE LIFE ZONE IN COSTA RICA

INTRODUCTION

It is well known that the tropical forests of the world are under siege. By some estimates 250,000 square kilometers of tropical forest are impacted by logging or converted to other land uses every year (Meyers, 1991;Veldkamp, 1992). Most of the world's attention has been focused on areas, such as Amazonia, where there are still vast areas of untouched forest. In these areas preservation can still save large tracts of forest. However, there are many areas in the tropics where much of the original tropical forest has already been converted to other uses. In Costa Rica, where about 22% of the country is in protected status (national parks, forest reserves, Indian reservations), (Hartshorn et al., 1982) only 28% of the country is still forested (Solórzano et al., 1991). This is in a country that still had 59% of its area in forest as late as 1966 (Solórzano et al., 1991).

Along with this drop in forest land there has been an equal rise in the area devoted to agricultural land in Costa Rica. However, not all classes of agricultural land have grown at similar rates. While the area of land in crops has remained fairly steady (increasing from about 0.45 million hectares to 0.6 million hectares from 1970 to 1989) the land in pasture has increased by 28% to about 1.8 million hectares (Solórzano et al., 1991). Much of this conversion of forest to pasture was encouraged by subsidies from the government. The incentives are much less attractive now and the rate of abandonment of degraded pastures has increased. Degraded pastures are defined here as having a loss in productivity resulting from a number of possible reasons, such as

compaction, loss of organic matter by erosion or oxidation and decreases in pH caused by accelerated leaching.

A number of authors have suggested that secondary forest succession in degraded pastures in Costa Rica is impaired (Fournier, 1990). Solórzano et al., (1991) suggests that potential forest growth on these pastures is reduced because of nutrient loss and soil compaction. Daubenmire (1972) found losses in organic matter and significant erosion in pastures in Guanacaste Province. Krebs (1975) also found losses in organic matter, nitrogen and pH in pasture soils in north-central Costa Rica. Some also believe that not only is productivity reduced on degraded pastures but that tree regeneration is itself delayed (Gutiérrez, 1994, personal communication).

To effectively study forest succession in abandoned pastures it is important to be able to classify pastures into levels of productivity or levels of degradation. Once this is done these pasture groups can be studied to see if there is indeed a regeneration problem on degraded pastures. Studying the soil characteristics of pastures with these different levels of productivity can also shed light on the causes of the degradation.

The study discussed in Part I compared paired plots of undisturbed forest and adjacent pasture in the Puriscal area of Costa Rica and found changes in several soil characteristics between the plots. Bulk density was higher and pH was lower in the pasture plots than in the forest plots. Pasture plots were also classified into three broad groups on the basis of the levels of erosion. There were also changes in some soil characteristics between their erosion groups. Clay content increased and organic carbon and total nitrogen decreased as erosion increased.

This study uses the data collected in Part I as input for a site-quality assessment model developed by Gutiérrez (Gutiérrez, 1991; Gutiérrez and Mize, 1993) for use in two life zones in Costa Rica. The Gutiérrez model will be described in the Materials and Methods section. Application of the model using the data from Part I will also be discussed.

The first objective of this study will be to use the Gutiérrez model to determine if there are significant differences in the operational factors between forest and pasture plots and also between erosion groups. Another objective will be to use the model to indirectly measure tree regeneration success by comparing the operational factors (synecological coordinates) calculated with the model with ecographs for ten plant species native to the life zone. The first hypothesis that will be tested is that the Gutiérrez site-quality assessment model will show that the soils of the pasture plots are degraded when compared to forest plots, as shown by the pasture plots having lower moisture and nutrient coordinates in the edaphic field and higher light and heat coordinates in the climatic field.

The second hypothesis is that the model will show an increasing amount of degradation moving from erosion group 1 to erosion group 3, as shown by a decrease in the moisture and nutrient coordinates in the edaphic field and an increase in the light and heat coordinates in the climatic field as erosion increases.

The third hypothesis is that the pasture plots will have impeded tree regeneration compared with the forest plots, as shown by the moisture, nutrient, light and heat coordinates of the pasture plots being outside the boundaries of the ecographs for ten selected tropical plant species.

The fourth hypothesis is that there will be an increasing impediment to tree regeneration as erosion increases in the pasture plots, as shown by the moisture, nutrient, light and heat coordinates of the three erosion groups being increasingly outside the ecographs of the ten selected tropical plant species as erosion increases from erosion group 1 to erosion group 2 to erosion group 3.

Success or failure of tree regeneration as discussed in all of the above hypotheses and in the following sections refers to success or failure of tree seed germination.

MATERIALS AND METHODS

Introduction

The data used in this study came from a field project that was conducted between January and March, 1993 in the Puriscal region of Costa Rica. The study looked at the changes in soils between paired plots of pasture and undisturbed forest. Data were collected on twenty-four paired plots of forest and pasture, with a wide variety of slope angles, slope positions and aspects represented. The study area was in the Tropical Moist Forest, Premontane Belt Transition Life Zone (Tosi, 1969) and was centered about 30 km southwest of the capital, San José. Further discussion of the materials and methods used in the field study can be found in Part I.

The Gutiérrez Site-Quality Assessment Model

The site-quality assessment model as developed by Gutiérrez (Gutiérrez, 1991; Gutiérrez and Mize, 1993) for two life zones in Costa Rica combines the method of synecological coordinates (MSC) first developed by Bakuzis (1959) with physiognomic data. The MSC is an ordination technique that defines the quality of a site by developing synecological coordinates which are relative measures of the biotically effective part of the environment. The synecological coordinates are relative measures of the operational (environmental) factors of a site. The synecological coordinates used in the Gutiérrez study were moisture,

nutrients, heat and light. The coordinates have relative values of 1 to 5, with 1 being the lowest level of a factor and 5 being the highest.

Synecological coordinates are calculated by first estimating the coordinate scores for plant species found in a particular area using the expert opinion of botanists, taxonomists, etc. Then an inventory is done of the species present on sites from a wide variety of environmental conditions within an area. The inventory information is used to modify the initial coordinate scores. The modified synecological coordinates for a site are then averaged to obtain a site average synecological score.

Gutiérrez then relates the synecological coordinates (operational factors) of a site to the physiognomic characteristics using linear regression. Once the link is made between the species present on a site and the site characteristics the results become predictive. The characteristics of a site can be measured and a prediction made as to which plant species would best grow on that site, ie. the site quality would be determined. Gutiérrez and Mize (1993) and Gutiérrez (1991) give an overview of the theoretical aspects of this method of determining site quality.

Gutiérrez recommends against using his site-quality model as it currently stands because the data set used to develop the regression equations was small. Some of the physiognomic factors used in the equations were represented by only a few sites. However, it was thought that the model could be successfully used in this current study because many of the paired plots from the field study were in close proximity to the sites used by Gutiérrez.

The Gutiérrez model initially used ten physiognomic factors in the regression equations that calculated the synecological coordinates. They were

soil order, heat (temperature regime for the area), slope position, slope shape, slope aspect, soil texture, soil depth, organic matter, compaction and soil moisture. The site factors and the classes within each factor can be found in Appendix 3 Only seven physiognomic factors were used in this study. Slope shape and soil compaction were not included in the final regression equations for the Tropical Moist Forest, premontane belt transition because the two factors did not contribute significantly to the equations. The heat physiognomic factor was not used because all of the plots are within the same life zone and therefore had similar temperature regimes. The heat physiognomic factor is different than the heat synecological coordinate and should not be confused with it.

Tables were developed by Gutiérrez (Gutiérrez, 1991; Gutiérrez and Mize, 1993) that simplified calculating the four synecological scores. These tables can be found in Appendix 4 The tables were used to calculate the synecological scores for the forest and pasture plots in the twenty-four paired plots and the three erosion groups using the physiognomic data collected in the field study. Soil moisture was not measured in the field study, however, it was estimated for use in the Gutiérrez model by assuming that all of the forest plots were moist and that all of the pasture plots were dry. There were two reasons for making this assumption. First, the soil moisture definition used in the Gutiérrez model was a poor definition for soil moisture. The soil moisture was determined by how the soil of a particular site molded in ones hand at the time of sampling. The definition did not take into account the antecedent moisture conditions or moisture holding properties of the soil. Second, it was observed that the surface soil in the forest plots consistently felt more moist than the surface soil in the pasture plots. Given the crudity of the soil moisture definition in the model it

was thought that the crude observation of soil moisture in the field study was sufficient to classify the soil moisture status of the plots.

Soil depth was estimated using information on the surface exposure of bedrock at a plot and on whether bedrock was reached when collecting the soil samples. Only the regression equation for light used the soil depth information. The two classes used in the equation were shallow (depth less than or equal to 20 cm) or otherwise (included all other soil depths).

The organic carbon measurements from the 0-15 cm depth, taken in the field study, were converted into organic matter levels for use in the model by multiplying by two (Nelson and Sommers, 1982).

The synecological coordinate scores for the twenty-four paired plots were averaged by forest plots, by pasture plots and by erosion groups. The means of the forest and pasture plots were compared for significant differences using paired t-tests. The means of the three erosion groups were also compared for significant differences using the general linear model and least-squared means. The means of the forest and pasture plots and the tree erosion groups were plotted on ecographs of the edaphic and climatic fields of the life zone to graphically display differences in the synecological scores.

The means of the forest and pasture plots and the three erosion groups were also plotted on ecographs of three plant species for the life zone. The ecographs were constructed using unpublished data from Gutiérrez (1994). The three plant species were selected to represent species with three different types of ecographs. One species was adapted for pioneering forest gaps (*Solanum brenesii*), one species for low requirements for moisture and nutrients (*Garcinia intermedia*) and one species for high requirements for moisture and nutrients

(*Swartzia picramnoides*). The relationship of the forest and pasture plot means and the erosion group means to the plant ecographs was examined to determine if the means fell within or outside of the boundaries of the ecographs. Any plot or group means that fell outside the boundaries of any of the ecographs indicated that that plot or group had physiognomic factors that would prevent regeneration of the effected species.

RESULTS

Forest, Pasture and Erosion Group Comparisons

The mean synecological scores for the forest and pasture plots are in Table 6. A complete listing of the data used in this analysis along with the synecological scores for each plot can be found in Appendix 5. There were marked differences in all four synecological scores between the forest and the pasture plots. The moisture score for the forest plots was greater (2.56) than the score for the pasture plots (2.26). Likewise, the nutrient score for the forest plots was higher (2.55) than the score for the pasture plots (2.28). Both the heat and light scores for the forest plots (3.27 and 3.76, respectively) were lower than the scores for the pasture plots (3.56 and 4.10, respectively). The differences between the forest and pasture plots were primarily caused by differences in the organic matter content and from differences in the moisture content of the forest and pasture plots.

The means for the moisture, nutrient, heat and light coordinates for the three erosion groups are in Table 7. The moisture and nutrient scores slightly declined as the level of erosion increased, though, at the 0.25 level, there were no statistically significant differences between erosion groups. The moisture score for erosion group 1 was 2.33. The score for erosion group 2 was 2.24, and for erosion group 3 the score was 2.17. The nutrient score for erosion group 1 was 2.35; for erosion group 2, 2.27; and for erosion group 3, 2.18.

Table 6. The mean synecological scores for moisture, nutrient, heat and light for the forest and pasture plots using the Gutiérrez site-quality assessment model

Plot	Moisture	Nutrient	Heat	Light
Forest	2.56**	2.55**	3.27**	3.76**
Pasture	2.26**	2.28**	3.56**	4.10**
SE[1]	0.03	0.03	0.02	0.01
P-value[2]	0.0001	0.0001	0.0001	0.0001

** significantly different at the 0.01 level
1 SE is the standard error of the difference between the forest and pasture plots from a paired t test
2 tthe P-value is the probability of a greater t value under the null hypothesis of no treatment differences

There were no statistically significant differences between the heat scores for the erosion groups at the 0.25 level. The score for erosion group 1 was 3.51. The score for erosion group 2 was 3.54, and the score for erosion group 3 was 3.66. There were notable differences between the light scores for the erosion groups. The score for erosion group 1 (3.92) was significantly different from the score for erosion group 2 (4.22) and also was different than the score for erosion group 3 (4.30). The score for erosion group 2 was not significantly different than the score for erosion group 3.

Figure 3 shows the ecograph of the edaphic field and Figure 4 shows the ecograph of the climatic field for the Tropical Moist Forest, premontane belt transition Life Zone. The outer boundaries of the ecographs mark the limits of the synecological coordinates for the life zone as found by Gutiérrez (1991). The

Table 7. The means of the synecological coordinates of moisture, nutrient, heat and light for the three erosion groups using the Gutiérrez site-quality assessment model

Erosion Group	Moisture	Nutrient	Heat	Light
1	2.33A[1]	2.35A	3.51A	3.92A
SE[2]	0.10	0.10	0.08	0.13
n=11				
2	2.24A	2.27A	3.54A	4.22B
SE	0.13	0.13	0.10	0.17
n=6				
3	2.17A	2.18A	3.66A	4.30B
SE	0.12	0.12	0.10	0.16
n=7				

1 means with different letters are significantly different at the 0.25 level
2 SE is the standard error for each erosion group

boxes that make up the ecograph result from an attempt by Gutiérrez to simplify the plotting of the synecological coordinates. Instead of creating an ecograph by connecting points of equal probability, the synecological scores are rounded to the nearest 0.5 units and placed in the appropriate box. Each box is 0.5 by 0.5 units in size.

In the ecographs in Figures 3 and 4, the coordinates of the forest and the pasture plots are plotted. The forest and pasture plots are together in the same box in both ecographs. In the edaphic ecograph in Figure 3, the rounded forest plots coordinates are 2.5 and 2.5 for the moisture and nutrient scores, respectively and the rounded pasture plots coordinates are also 2.5 and 2.5, respectively. Rounding the scores to the nearest 0.5 units appears to eliminate

the differences between forest and pasture plots, even though that is just a result of the graphing technique used in the figures.

In the climatic ecograph in Figure 4, the rounded heat and the light scores for the forest plots are 3.5 and 4.0, respectively. The rounded pasture plots coordinates are 3.5 and 4.0, respectively, as well. As in the edaphic field ecograph, rounding the scores to the nearest 0.5 units appears to eliminate the differences between forest and pasture plots.

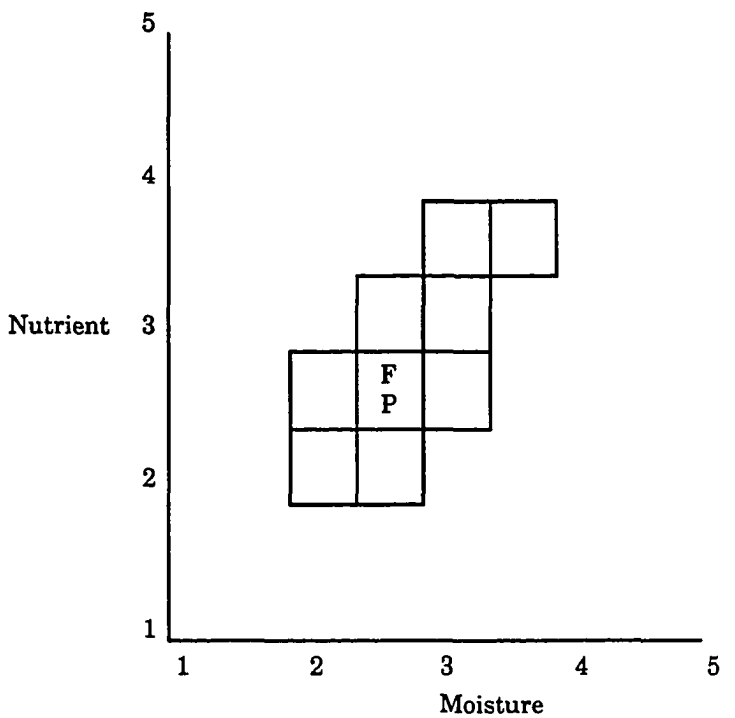

Figure 3. The ecograph for the edaphic field for the Tropical Moist Forest, Premontane Belt Transition Life Zone, with moisture and nutrients as the coordinates, indicating the locations of the mean scores for the forest plots (F) and the pasture plots (P).

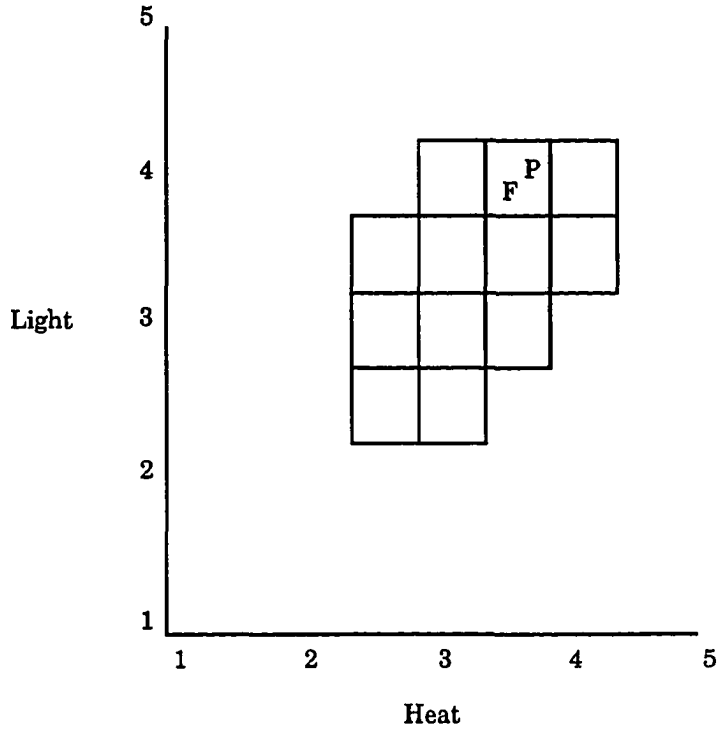

Figure 4. The ecograph for the climatic field for the Tropical Moist Forest, Premontane Belt Transition Life Zone, with heat and light as the coordinates, indicating the locations of the mean scores for the forest plots (F) and the pasture plots (P).

The edaphic ecograph for the three erosion groups is in Figure 5. The rounded moisture and nutrient scores for erosion group 1 are 2.5 and 2.5, respectively. The rounded scores for erosion group 2 are 2.0 and 2.5, respectively, and the rounded scores for erosion group 3 are 2.0 and 2.0. Even though the rounded scores for the erosion groups place the groups in different boxes there is still no significant difference between the moisture and nutrient scores of the groups.

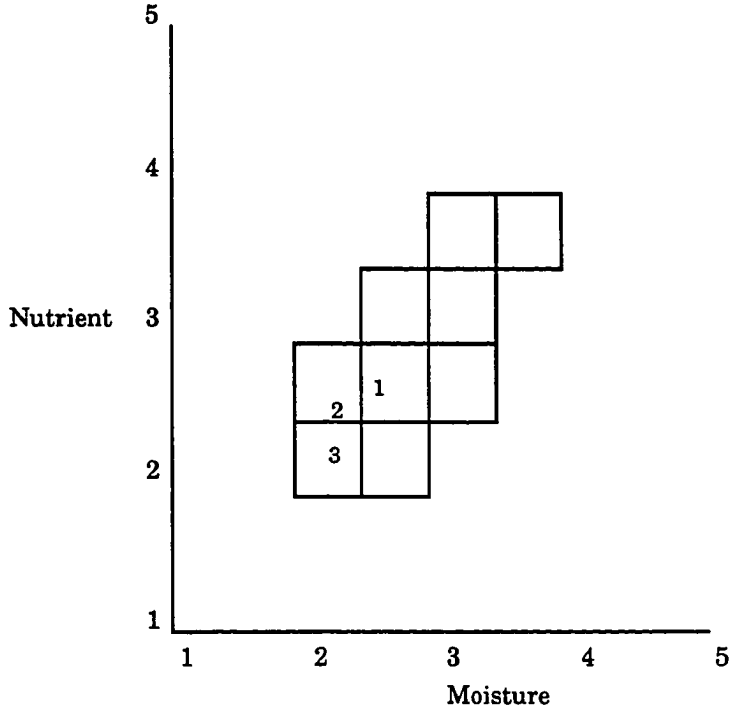

Figure 5. The ecograph for the edaphic field for the Tropical Moist Forest, Premontane Belt Transition Life Zone, with moisture and nutrient as the coordinates, indicating the locations of the mean scores for erosion group 1 (1), erosion group 2 (2) and erosion group 3 (3).

The ecograph for the climatic field for the three erosion groups is in Figure 6. The heat and light scores for erosion group 1 are 3.5 and 4.0, respectively. The scores for erosion group 2 are also 3.5 and 4.0, respectively, while those for erosion group 3 are 3.5 and 4.5, respectively. The light score for erosion group 3 places the group outside of the boundaries of the climatic ecograph. As mentioned before, there were no statistically significant differences between the

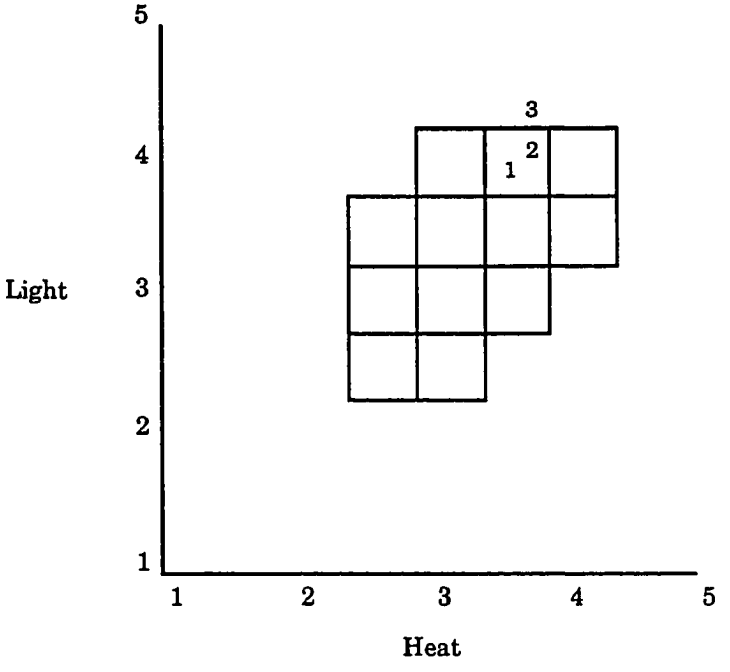

Figure 6. The ecograph for the climatic field for the Tropical Moist Forest, Premontane Belt Transition Life Zone, with heat and light as the coordinates, indicating the locations of the mean scores for erosion group 1 (1), erosion group 2 (2) and erosion group 3 (3).

heat scores of the three erosion groups. However, for the light score, erosion group 1 and erosion group 3 were significantly different.

Plant Ecograph Comparisons

The mean scores for the four synecological coordinates for the forest and pasture plots and the mean scores of the three erosion groups were plotted on the

edaphic and climatic ecographs for the three species; *Solanum brenesii*, *Garcinia intermedia* and *Swartzia picramnoides*. In each of the following three figures the forest and pasture scores and the erosion group scores are plotted the same as in Figures 3 through 6. The shaded boxes within each ecograph represent the parts of each ecograph occupied by the respective species.

Figure 7 shows the forest and pasture scores and the erosion group scores plotted on the edaphic and climatic fields for *Solanum brenesii.* The portions of the edaphic and climatic fields occupied by *Solanum brenesii* are shaded. In the edaphic field, the forest and pasture scores and all three of the erosion group scores fall within the shaded portion of the ecograph. In the climatic field, the forest and pasture scores and the scores for erosion groups 1 and 2 fall within the shaded portion of the ecograph, while the erosion group 3 score fall outside the boundary of the ecograph. The asterisk next to the erosion group 3 score, in the climatic field, indicates that the possible light and heat scores for *Solanum brenesii* fall somewhat outside the boundaries of the Life Zone ecograph.

Figure 8 shows the forest and pasture scores and the erosion groups scores plotted on the edaphic and climatic fields for *Garcinia intermedia*. The scores for forest, pasture and the three erosion groups all fall within the shaded boxes in the edaphic field. The scores for forest, pasture, erosion group 1 and erosion group 2 fall within the shaded boxes of the climatic field, while the score for erosion group 3 falls outside the life zone ecograph boundaries. However, the erosion group 3 score does fall within the species ecograph boundary of the possible heat and light scores for *Garcinia intermedia*, as indicated by the asterisk.

Figure 9 shows the forest, pasture and erosion group scores plotted on the edaphic and climatic fields for *Swartzia picramnoides*. In the edaphic field, the scores for forest, pasture and erosion group 1 fall within the shaded boxes, but the scores for erosion groups 2 and 3 fall outside of the shaded boxes. In the climatic field the scores for forest, pasture, and all three erosion groups fall outside the shaded boxes.

The boundaries of the ecographs of the three species may be poorly defined because of the small sample sizes. The ecographs for *Solanum brenesii* were constructed using 16 observations, the ecographs for *Garcinia intermedia* with 31 observations and the ecographs for *Swartzia picramnoides* using 11 observations.

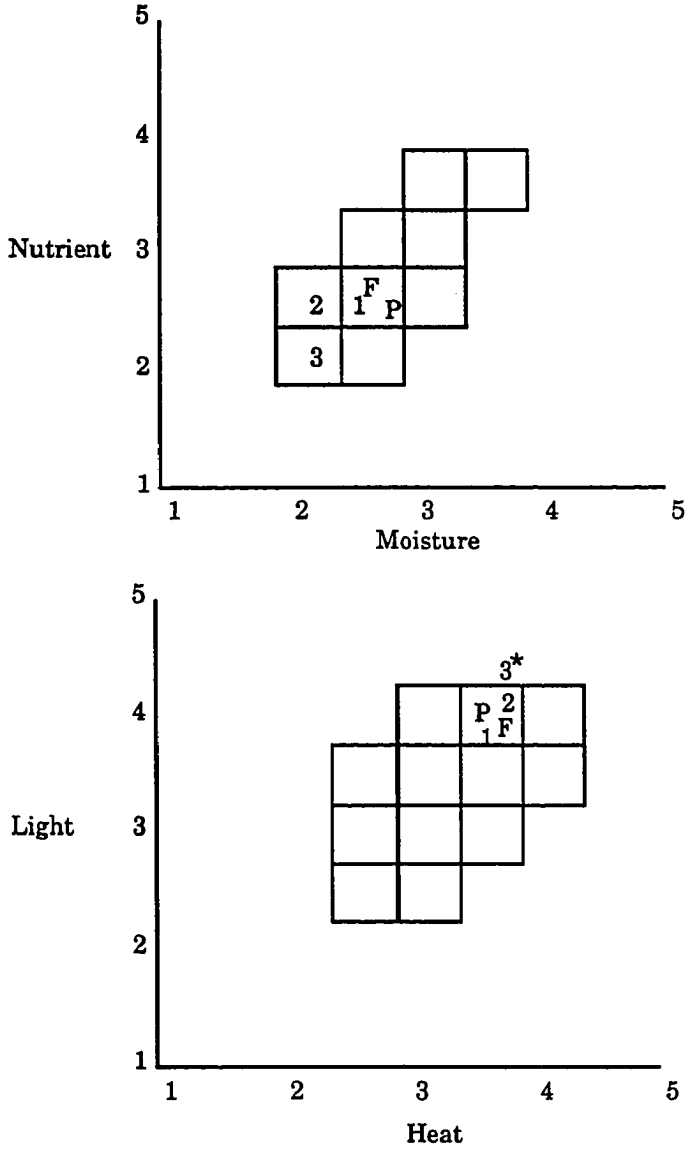

Figure 7. The edaphic and climatic fields for the Tropical Moist Forest, Premontane Belt Transition Life Zone with the range of *Solanum brenesii* within the ecograph boundaries indicated by the shaded boxes and the range outside the ecograph indicated by an asterisk. The position of the forest scores is indicated by an F, pasture by a P, and each erosion group by its number.

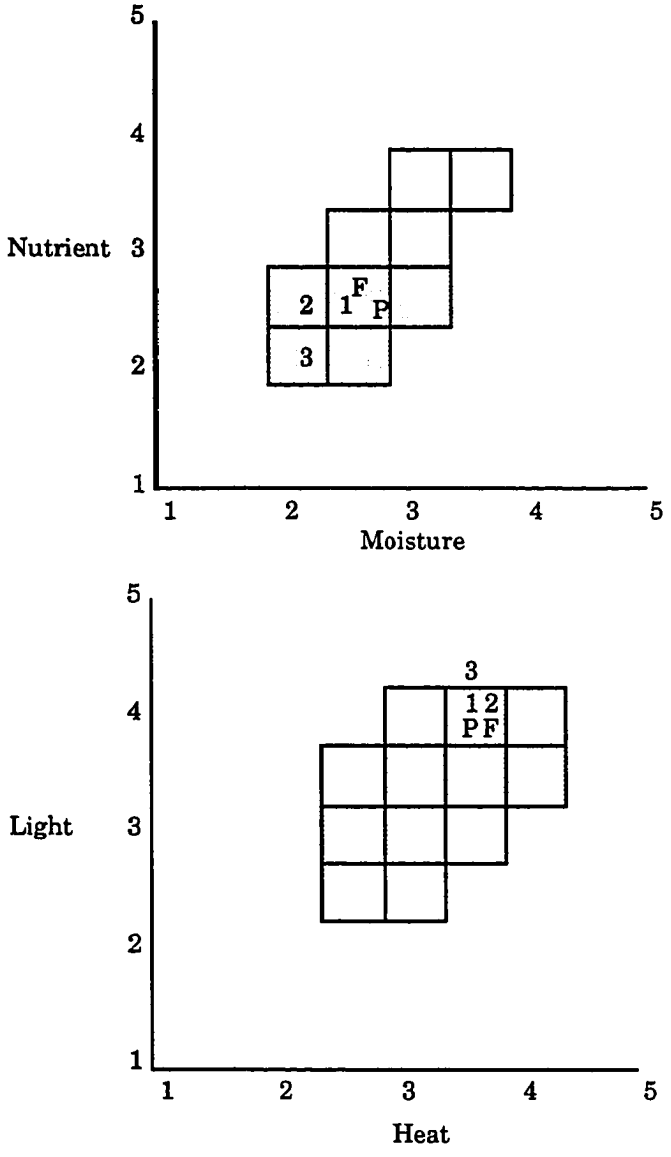

Figure 8. The edaphic and climatic fields for the Tropical Moist Forest, Premontane Belt Transition Life Zone with the range of *Garcinia intermedia* within the ecograph boundaries indicated by the shaded boxes. The position of the forest scores is indicated by an F, pasture by a P, and each erosion group by its number.

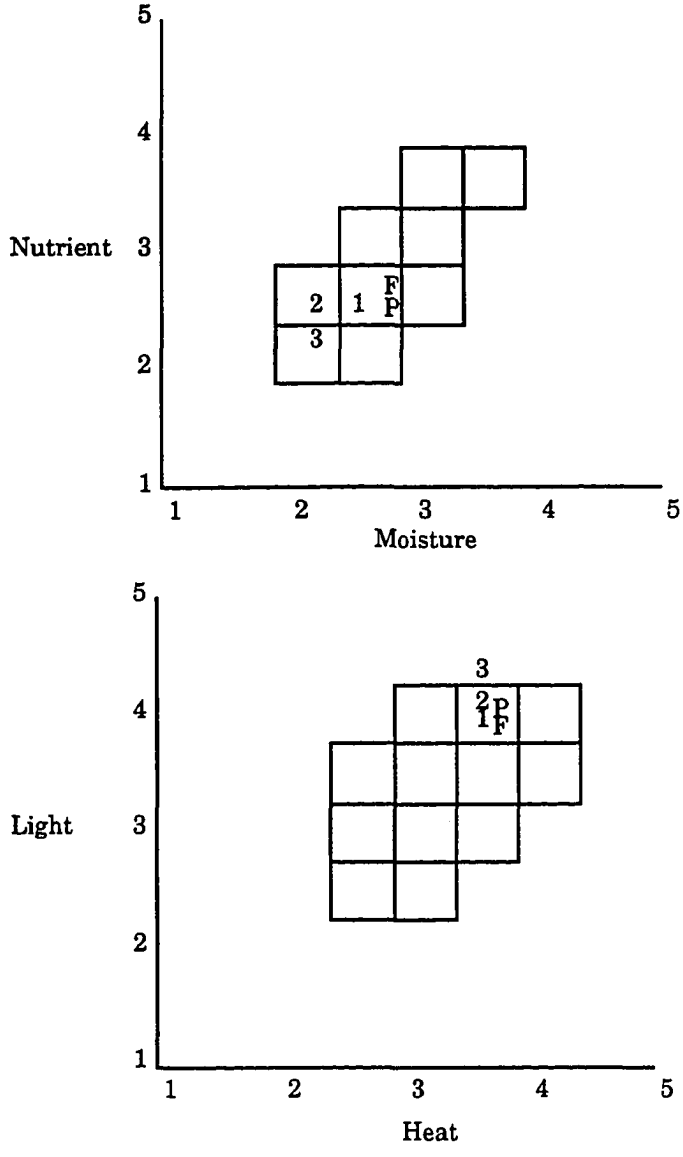

Figure 9. The edaphic and climatic fields for the Tropical Moist Forest, Premontane Belt Transition Life Zone with the range of *Swartzia picramnoides* within the ecograph boundaries indicated by the shaded boxes. The position of the forest scores is indicated by an F, pasture by a P, and each erosion group by its number.

DISCUSSION

Forest and Pasture Differences

It was hypothesized in an preceding section that the Gutiérrez site-quality assessment model would show that the soils of forest and pasture plots were degraded on the basis of lower moisture and nutrient scores and greater heat and light scores for the pasture plots. This appears to be the case. Model results indicated that there were statistically significant differences between the synecological scores for the forest and the pasture plots. The model results seem to indicate that there has been some soil degradation in the pasture plots compared to the forest plots. However, is the amount of degradation sufficient to impede tree regeneration? A general answer to that question is impossible. The question must be asked in light of the regeneration requirements of individual tree species. For example, compare the regeneration requirements (or tolerances) of the temperate species, sandbar willow (*Salix interior*) and black walnut (*Juglans nigra*). The sandbar willow can tolerate the extreme environmental conditions of a bare sandbar where the surface temperature of the exposed sand can become quite high and where the poor water holding capacity of the sand can result in low soil moisture levels near the surface. The black walnut cannot tolerate the high surface temperatures and the low soil moisture of the sandbar and would succumb to the rigors of the site.

Another of the hypotheses of this study was that the soil characteristics of the pasture plots would impede regeneration, as shown by the the synecological scores for the pasture plots falling outside of the ecograph boundaries of the

three representative plant species. The hypothesis should be rejected because there were no differences in the positions of the forest and pasture plots relative to the boundaries of the ecographs of the three species. In the edaphic field, the coordinate scores for the forest and pasture plots fell within the ecograph boundaries of the three species. In the climatic field, the coordinate scores for the forest and pasture plots fell completely within the ecograph boundaries for *Solanum brenesii* and *Garcinia intermedia*, while the scores fell completely outside of the ecograph boundary for *Swartzia picramnoides*. Both the forest and the pasture plots were suitable for regeneration of *Solanum brenesii* (a pioneer species) and *Garcinia intermedia* (a species with low moisture and nutrient requirements), while neither plot was suitable for the regeneration of *Swartzia picramnoides* (a species with high moisture and nutrient requirements).

While the slight soil degradation in the pasture plots did not seem to increase regeneration difficulties for the three species, it is possible that there are some tree species that have very specific regeneration requirements and that would show a difference in regeneration success between the forest and tree plots. It is therefore useful to examine the soil characteristics that most influence the calculation of the synecological scores. The two most important characteristics were soil organic matter content and soil water content.

Organic matter content impacts the synecological coordinates in several ways. The moisture coordinate is impacted by the effect of organic matter on the infiltration rate and water retention characteristics of the soil. Organic matter in the soil strengthens soil aggregates (Bond, 1959). Strong soil aggregates do not break apart easily and therefore sealing of the soil surface is inhibited and

water infiltration is maintained. Strong soil aggregates also resist destruction from the forces involved in wetting and drying cycles, animal treading, etc. and therefore the water retention characteristics of the soil are not reduced (Jury et al., 1991).

The lower organic matter content of the pasture plot soils implies that there has been some loss of soil aggregate strength with perhaps a greater tendency for surface sealing in the those soils and a lower ability to retain moisture. The moisture content of the soil impacts greatly on the ability of seeds to imbibe the water necessary for germination. The small reduction in moisture in the pasture plots may slow imbibition of water into seeds when compared to the forest plots.

Organic matter influences the nutrient coordinate by providing exchange sites for nutrient ions. Small changes in the organic matter content of a soil can impact on soil nutrient retention because of the high cation exchange capacity of organic matter. The higher organic matter content of the forest soils would imply a greater ability to retain nutrients. However, the higher cation exchange capacity has no impact on seed germination because the nutrients needed in germination are supplied by the seed itself (Kramer and Kozlowski, 1979). Therefore, any difference in nutrients between the forest and pasture plots will have no impact on tree seed germination.

One way organic matter content can impact the heat coordinate is by indirectly influencing the water content of the soil. The higher soil water contents associated with higher organic matter contents increases the specific heat of the soil and greatly increases the capacity of the soil to store heat. Greater heat movement into the soil results in lower surface soil temperatures

when the soil is exposed to sunlight. In areas exposed to direct sunlight surface soil temperatures may sometimes become high enough to inhibit seed germination (Smith,1986). Higher organic matter contents may prevent this by lowering the surface soil temperatures. In the case of this study, the higher organic matter contents of the forest plots may result in greater seed germination rates than in the pasture plots, when solar radiation conditions are equal.

Organic matter in surface soil may also influence the heat coordinate by modifiying pore size distribution and thereby changing the heat conductivity. Higher organic matter content in the surface soil can increase the porosity, which would result in a decrease in heat conduction. Surface temperatures would be higher in this case when the soil is struck by sunlight because less heat would be conducted away from the surface.

Organic matter content may impact the light coordinate by influencing the albedo of the soil. The higher the organic matter content of a soil the lower the reflectance (Lillesand and Kiefer, 1979). The overall light intensity of a bare soil exposed to sunlight would decrease as the organic matter content of the soil increased. The higher organic matter content of bare soil in the forest plots will reflect less light than bare soil in the pasture plots, light conditions being equal. However, the differences in albedo should have little to no influence on seed germination because, while light intensity may be changed, the spectral quality of the light should not be modified. For most seeds, spectral quality of the light is more important than a relatively small decrease in light levels.

The changes in albedo that accompany changes in organic matter content can also influence the heat load of soil. The heat load of the soil depends, partly,

on the amount of solar radiation that is absorbed. The lower albedo of soil with higher organic matter content results in greater absorption of solar radiation and greater heat load in the soil. The decrease in albedo can counteract the effect of higher organic matter content on soil moisture and heat movement.

Soil moisture impacts the synecological coordinates in several ways. It influences the moisture and heat coordinates, however, its influence on those coordinates has already been discussed in the above section on organic matter. Therefore, only the impact of soil moisture on the nutrient coordinate will be discussed below. Soil moisture levels possibly can impact the nutrient coordinate by influencing the ionic strength of the soil solution and thereby increasing the solute water potential. If the ionic strength of the soil solution becomes too great passive transport of nutrients into a plant can diminish. At even greater ionic strengths active nutrient transport can be reduced as well. However, this only becomes a problem in very dry soils or in saline soils. Besides, as has been mentioned previously, the nutrient content of the soil is not important to seed germination. Therefore, the lower value of the nutrient coordinate in the pasture plots does not impact germination.

Soil moisture content may influence the light coordinate by modifying the albedo of the soil. A moist soil will reflect less light than a dry soil (Lillesand and Kiefer, 1979). This phenomenon would most likely have little to no influence on seed germination first, because the amount of light reflected by the soil is a small component of the overall amount of light reaching the plant and second, while the light level might decrease with increased soil moisture, the spectral quality of the light would be mostly unchanged. The lower light

coordinate value for the pasture plots would have little to no impact on seed germination.

The changes in albedo that accompany changes in soil moisture can also influence the heat load of soil. The heat load of the soil depends, partly, on the amount of solar radiation that is absorbed. The lower albedo of moist soil results in greater absorption of solar radiation and greater heat load in the soil.

Erosion Group Differences

Two hypotheses were proposed concerning the impact of the three erosion groups on soil degradation and plant regeneration. The first hypothesis was that the Gutiérrez site-quality assessment model would show increased amounts of soil degradation as the level of erosion increased from erosion group 1 to erosion group 3, as shown by a decrease in the moisture and nutrient coordinates and by an increase in the heat and light coordinates. The hypothesis should be, for the most part, rejected. Model results found that there were no statistically significant differences between the moisture, nutrient and heat coordinates of the three erosion groups. However, there was a statistically significant difference in the light coordinate between erosion group 1 and erosion group 3. The light coordinate for erosion group 3 was greater than for erosion group 1. The light coordinate value for erosion group 2 was not different from the values for erosion group 1 or erosion group 3. In the case of the light coordinate the above hypothesis can not be rejected. The soils in erosion group 3 may be degraded.

The second hypothesis made a statement concerning the impact of degradation on plant regeneration. It stated that there would be a greater impediment to regeneration as erosion increased, as shown by the moisture, nutrient, heat and light coordinates being increasingly outside of the ecograph boundaries of the three representative plant species. The hypothesis cannot be completely rejected. The moisture and nutrient coordinates for the three erosion groups all fell within the ecographs for the three plant species and therefore, the coordinates for the erosion groups did not impede regeneration. However, in the climatic field, the heat and light coordinates for erosion group 3 did fall outside the boundary of the ecograph for *Garcinia intermedia*. In this case, the level of degradation in erosion group 3 may be sufficient to prevent regeneration of the species. However, a definitive statement about regeneration success cannot be made because of two factors. First, there was no significant difference between the mean heat and light coordinate scores of erosion groups 2 and 3. The difference between erosion groups 2 and 3 in Figure 8 is only a result of the graphing technique used and not a real difference. Second, the boundary for the species ecograph for *Garcinia intermedia* is unclear because of the small sample size used by Gutierrez to develop the ecographs. The heat and light coordinates for the three erosion groups fell completely within the ecograph boundary for *Solanum brenesii* and fell completely outside of the boundary for *Swartzia picramnoides*. The levels of degradation in the erosion groups had no impact on regeneration of these two species.

As with the discussion of forest/pasture differences from above, there were two soil characteristics that primarily impacted the coordinate scores: organic matter and soil moisture. The impact of organic matter and soil moisture on the

moisture and nutrient coordinates will not be discussed because neither of those coordinates were significantly different between the three erosion groups. Even though the heat coordinate was not significantly different between erosion groups it will still be considered because of its interaction with the light coordinate in the climatic field ecographs. Organic matter impacted the heat coordinate by influencing heat movement in the soil and the light coordinate by influencing the albedo and therefore heat of the soil. However, as with the forest/pasture discussion, only changes in the heat coordinate seemed to impact seed germination. The light coordinate did not impact germination. The lower organic matter levels in erosion group 3, compared to erosion group 1, could result in greater heat which could cause seed death by overheating or seedling death by girdling at the root collar. These may be the reasons that *Garcinia intermedia* cannot regenerate in erosion group 3 conditions.

Soil moisture impacted the coordinates in similar ways to organic matter. Soil moisture impacted the heat coordinate by its influence on heat movement in the soil. Soil moisture impacted on the light coordinate by influencing albedo. As above, only the heat coordinate impacts seed germination. Again, the lower soil moisture content in erosion group 3 may be part of the reason for the inability of *Garcinia intermedia* to regenerate.

Model Limitations

The site-quality assessment model developed by Gutiérrez (Gutiérrez, 1991; Gutiérrez and Mize, 1993) shows much promise in identifying sites that have been degraded and that might have limitations on tree regeneration. The

methodology overcomes the problems normally associated with attempting to assess site quality in tropical forests (one problem being the inability to use site index as a measure of site quality on the uneven aged stands that predominate in the tropics). However, there are several procedural problems with the current model. Several of the problems arise because of the limited data set used for developing the equations.

The small data set and the limited variety of plots sampled leads to the organic matter category being relatively insensitive to changes in organic matter. There are only two levels of organic matter. One level for organic matter contents above 10% and the other for organic matter contents below 10%. In the field study discussed in Part I, the organic matter contents of 36 of the 48 plots were below 10%. The range covered just by these plots was from a high of 9.8% to a low of 3.4%. A larger data set, covering many more plots, would most likely lead to organic matter contributing more to the regression equations for the synecological coordinates.

The narrow range of plots used to develop the regression equations in the Gutiérrez model also resulted in soil compaction having no impact on the synecological scores. Soil compaction did not contribute significantly the development of the regression equations and was therefore not included as a factor in them. A larger data set, covering a greater variety of plots, would probably result in soil compaction being included in the regression equations.

Most of the differences between forest,pasture and erosion group synecological scores can be explained by the differences in soil moisture levels and by differences in organic matter contents (even though the categories for organic matter were too broad and insensitive). However, using the soil

synecological scores. The three categories were chosen because of the simplicity of measurement (Gutiérrez and Mize, 1993), however, the model's sensitivity may be impaired by this simplification. Second, the method used for measuring the impact of soil moisture on plant growth is flawed. The method for sampling soil moisture measures current moisture levels and does not measure the soil moisture available to a plant throughout the year. A better method of determining soil moisture throughtout the year should be developed and integrated into the regression equations. One suggested method would be to link changes in bulk density to changes in the water holding capacity of the soil using regression equations.

CONCLUSIONS

The Gutiérrez site-quality assessment model was used to examine differences in the operational factors of moisture, nutrients, heat and light for the forest and pasture paired plots and for the three pasture erosion groups. The operational factors (called synecological coordinates in the model) were calculated for each plot and then differences were examined. It was found that there were statistically significant differences between forest and pasture plots for all of the four synecological coordinates. The moisture and nutrient coordinates were lower, while the heat and light coordinates were larger in the pasture plots. The coordinates for the forest and pasture plots were plotted on ecographs of the plant species to see whether the plots fell within or outside of the boundaries of the ecographs. Any plot falling outside of the boundary of one or more of the ecographs would indicate that operational factors in that plot were sufficient to prevent regeneration of those species. The coordinates for both the forest and the pasture plots fell within the boundaries of all three species, indicating that the pasture plots had not degraded enough to prevent regeneration.

The synecological coordinates of the three erosion groups were also compared. The moisture, nutrient and heat coordinates of the three groups were not statistically different. However, the light coordinates of erosion group 1 and erosion group 3 were different. When the heat and light coordinates were plotted on the ecographs of the three plant species erosion group 3 was outside the boundary of the ecograph for *Garcinia intermedia*. This indicated that for this species, and other species with similar ecographs, regeneration would be

impeded on erosion group 3 plots. The main soil characteristics impacting on the degradation of the erosion group 3 plots are organic matter and soil moisture. The two characteristics impact on the light coordinate by influencing the albedo of the soil. Further field research will need to be done to confirm the findings of this study, but at present the Gutiérrez site-quality assessment model seems to indicate that overall the level of soil degradation in pastures in the Puriscal region of Costa Rica is low enough that regeneration is not impeded. However, on heavily eroded pastures there appears to be sufficient degradation to limit regeneration for some species.

The Gutiérrez model has great potential for addressing the problem of identifying sites with tree regeneration problems. The model is specifically designed to determine soil quality for forestry. However, the model is currently limited because the equations were developed using a very small data set and because there are a few problems with the categories that are used in the model. The model should prove useful when the minor flaws are corrected. Further research should be done to enhance the effectiveness of the model for use in Costa Rica. Larger data sets can be collected from a wider variety of sites in the life zone so that the regression equations would be more sensitive. The research could also be expanded to other Life Zones in Costa Rica where soil degradation is also occurring.

GENERAL SUMMARY

Soil Degradation

Two studies were presented in this dissertation. The first study was conducted from January to March of 1993 in the Puriscal region of Costa Rica. The field study examined the soil characteristics of paired plots of forest and pasture. One of the hypotheses of this study was that there were significant changes in the soils of pastures when compared to the undisturbed forest soils. This hypothesis could not be completely rejected. There were significant differences between pasture and forest soils in bulk density and pH. As was expected, the bulk density of pasture plots was higher than that in the forest soils. Compaction of the pasture soils by cattle was the obvious cause of the higher bulk density. The pH of the pasture soils was lower than that in the forest soils. The lower pH was attributed to greater weathering of the pasture soils.

Clay content, organic carbon levels and total nitrogen levels were similar in the forest and pasture soils. A simple model of soil carbon accumulation was used to explain the similarities. While tropical forests contribute higher amounts of organic matter to the soil than pastures, the forests also have higher decomposition rates than pastures. These two factors result in the total accumulation of organic matter being similar in forest and pasture.

The second hypothesis stated that overstocking in some of the pastures would result in those pastures having greater degradation. The pasture plots were placed into three erosion groups on the basis of visibly observable erosion characteristics. The characteristics were "extent and depth of cattle paths",

"disturbance of the grass cover by trampling and the extent of grazing-step development" and "the amount of bare ground in the steps". There were significant differences in soil characteristics between the three erosion groups. Bulk density and pH were similar between groups, but clay content, organic carbon and total nitrogen differed between groups. Clay content increased from erosion group 1 to erosion group 3, organic carbon levels were highest in erosion group 1 and decreased moving to erosion group 3. Total nitrogen followed the same trend as organic carbon.

An unexpected result was that the organic carbon and total nitrogen levels in erosion group 1 were higher than in the undisturbed forest. This appeared to be mostly an artifact of the method used to calculate organic carbon and total nitrogen per hectare. Some of the increase might also be explained by the increase in the rate of movement of carbon and nitrogen through the herbivore pathway instead of through the litter pathway. Greater amounts of nitrogen were also diverted to the herbivore pathway. The two causes could not be separated with the data collected.

The declines in organic carbon and total nitrogen and the increase in clay content moving from erosion group 1 to erosion group 3 were attributed to an increase in erosion resulting from an increase in the stocking rate of cattle.

Site-Quality Assessment

The second study used a site-quality assessment model developed by Gutiérrez (Gutiérrez,1991; Gutiérrez and Mize, 1993) for use in two life zones in Costa Rica to examine differences in the operational factors between forest plots, pasture

plots and the three erosion groups. Soil characteristics were related to the operational factors which were in turn related to speculative changes in tree regeneration. The data collected from the first study were used in this study.

The operational factors (synecological coordinates) for the forest and pasture plots were compared. All four coordinates of moisture, nutrient, heat and light had a statistically significant difference. However, the coordinates were compared to the ecographs of three plant species and it was found that neither the forest or the pasture plots fell outside the boundaries of the ecographs. This indicated that the soil conditions of neither the forest or the pasture plots would limit regeneration.

The synecological coordinates of the erosion groups were likewise compared. The only difference was in the light coordinate. Erosion group 1 was different than erosion group 3. This difference was clear when the coordinates were plotted on the ecographs of the three species. The climatic coordinates for erosion group 1 fell within the ecograph boundary of *Garcinia intermedia*, while the coordinates of erosion group 3 fell outside of the boundary. This indicates that for this species, and other species with similar ecographs, regeneration is impeded for erosion group 3 plots.

The Gutiérrez model has great potential for assessing the impact of soil degradation on tree regeneration, but as the method now stands it has several weaknesses. The primary weakness is that the regression equations used in the method were developed with a small data set. This is not really a flaw because the study done by Gutiérrez was only an exercise in studying the feasibility of the model for use in Costa Rica. The authors fully intend to broaden the study and develop more accurate equations.

Additional Research

These two studies have raised as many questions as they have answered. Several areas still need to be studied before we have a firm idea of the extent of the regeneration problems in this part of Costa Rica. Natural regeneration could be studied on plots (where cattle are excluded), representing the three erosion groups, to directly answer the question of whether regeneration is delayed or impeded on some pastures. In pastures distant from natural seed sources the same question can be addressed by planting tree seeds and observing germination. Additional soil characteristics could be measured in these studies to determine which characteristics (if any) are causing the problem. If the studies point to soil characteristics not being an impediment to regeneration then another study could look at the source of propagules in pastures and whether tree propagules are limited.

Additional studies could compare nutrient cycling in paired forest and pasture plots and determine how changes in stocking rates influence that cycling. Erosion could also be directly studied in pastures and related to changes in stocking levels.

The Gutiérrez site-quality assessment model holds promise for identifying sites with tree regeneration problems. Further research should be done to enhance the effectiveness of the model for use in Costa Rica. Larger data sets can be collected from a wider variety of sites in the two life zones so that the equations would be more sensitive. The research could also be expanded to other life zones in Costa Rica where soil degradation is also occurring.

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APPENDIX 1

DATA FROM THE TWENTY-FOUR PAIRED PLOTS; INCLUDING THE TWENTY EXTENSIVELY SAMPLED PAIRED PLOTS AND THE MEANS OF THE FOUR INTENSIVELY SAMPLED PAIRED PLOTS

Plot	Vegetation type	Erosion Group	Altitude (meters)	Slope aspect	Slope angle (%)	Slope position	Soil type	Uncorrected bulk density (g cm-3)	Clay content (%)	Unadjusted total carbon (%)	pH	Unadjusted total nitrogen (mg N kg-1)
1	forest	n/a	820	north	50	shoulder	ultisol	0.62	26	4.50	4.00	4466
1	pasture	3	820	north	43	mid-slope	ultisol	0.67	32	2.90	4.40	3421
2	forest	n/a	920	north	44	mid-slope	ultisol	0.71	45	5.50	5.00	5039
2	pasture	3	920	north	44	mid-slope	ultisol	0.94	52	3.30	4.20	2838
4	forest	n/a	840	north	47	mid-slope	ultisol	0.58	15	6.60	5.10	8009
4	pasture	1	840	north	45	toe-slope	ultisol	0.70	6	7.30	4.90	7952
5	forest	n/a	900	north	38	mid-slope	ultisol	0.89	37	3.60	4.70	3097
5	pasture	1	900	north	46	shoulder	ultisol	1.02	31	4.10	4.60	2922
6	forest	n/a	880	north	57	shoulder	ultisol	0.85	32	3.50	5.00	3838
6	pasture	1	880	north	37	mid-slope	ultisol	0.86	26	4.90	4.80	4934
7	forest	n/a	880	north	36	shoulder	ultisol	0.85	42	4.10	4.80	3529
7	pasture	2	880	north	36	shoulder	ultisol	1.00	47	2.70	4.70	2710
8	forest	n/a	860	north	37	shoulder	ultisol	0.81	38	4.50	5.10	3940
8	pasture	2	860	north	38	shoulder	ultisol	1.00	34	3.50	4.70	3095
10	forest	n/a	820	east	21	shoulder	alfisol	0.74	40	5.80	4.80	4472
10	pasture	3	820	east	21	shoulder	alfisol	0.97	40	3.70	4.60	2913
11	forest	n/a	820	north	25	mid-slope	alfisol	0.67	46	4.30	5.20	3466
11	pasture	2	820	north	25	mid-slope	alfisol	0.94	50	3.20	4.90	2271
12	forest	n/a	840	east	47	mid-slope	alfisol	0.80	27	4.60	5.10	4227
12	pasture	1	840	east	49	mid-slope	alfisol	0.96	32	5.20	4.70	4598
13	forest	n/a	540	north	0	toe-slope	alfisol	1.08	22	3.20	5.40	2712
13	pasture	1	540	north	0	toe-slope	alfisol	1.18	27	4.20	4.80	3834
14	forest	n/a	880	west	60	mid-slope	ultisol	0.75	32	3.30	4.90	2958
14	pasture	2	880	west	70	mid-slope	ultisol	0.95	32	2.70	4.20	1708
16	forest	n/a	880	west	79	mid-slope	ultisol	0.73	19	2.40	5.30	3006
16	pasture	2	880	west	84	mid-slope	ultisol	0.88	28	2.10	5.10	2510
17	forest	n/a	660	east	4	toe-slope	alfisol	0.70	18	6.40	6.20	5032
17	pasture	3	660	east	5	toe-slope	alfisol	1.02	31	3.40	5.30	3696
18	forest	n/a	840	west	23	mid-slope	alfisol	0.80	41	4.80	5.10	3637
18	pasture	2	840	west	28	mid-slope	alfisol	0.95	37	3.90	4.80	2939
19	forest	n/a	700	south	58	shoulder	alfisol	1.13	16	4.20	5.70	3998
19	pasture	3	700	south	53	shoulder	alfisol	0.68	24	2.60	5.40	2630
21	forest	n/a	860	south	58	mid-slope	alfisol	0.74	20	2.90	5.10	3156
21	pasture	1	860	south	62	mid-slope	alfisol	0.99	17	3.30	4.90	3390
22	forest	n/a	640	west	32	mid-slope	alfisol	1.21	35	3.00	5.10	3182
22	pasture	3	640	west	36	mid-slope	alfisol	0.93	28	2.70	5.10	3270
23	forest	n/a	620	north	47	mid-slope	alfisol	0.94	34	2.20	5.30	2822
23	pasture	1	620	north	49	mid-slope	alfisol	1.06	36	2.40	5.10	2998
24	forest	n/a	700	north	58	mid-slope	alfisol	0.99	27	1.80	5.20	2225
24	pasture	1	700	north	61	mid-slope	alfisol	1.25	38	1.70	5.00	2372

APPENIDIX 2

DATA FROM THE FOUR INTENSIVELY SAMPLED PAIRED PLOTS

20	forest	n/a	840	east	70	mid-slope	alfisol	plot mean	0.94	28	2.30	5.20	2,253
								1	0.96	30	3.50	5.10	3,025
								2	0.94	24	3.30	5.20	2,235
								3	0.97	32	2.30	5.00	1,802
								4	1.03	30	2.40	5.20	1,497
								5	0.99	30	2.80	5.00	2,068
								6	1.08	40	1.50	5.00	1,601
								7	0.57	23	1.30	5.70	3,965
								8	0.89	25	3.80	5.50	3,743
								9	1.04	24	0.90	5.00	1,563
								10	0.97	19	0.90	5.10	1,029
20	pasture	1	840	south	71	mid-slope	alfisol	plot mean	0.97	17	2.60	4.80	2,788
								1	0.80	18	3.00	4.90	3,302
								2	1.16	17	3.30	4.80	3,752
								3	1.03	14	2.40	4.70	2,661
								4	0.98	23	1.50	4.80	1,552
								5	0.94	13	3.90	5.10	3,557
								6	0.93	18	2.90	5.00	2,709
								7	1.03	14	0.80	4.40	1,287
								8	0.89	15	2.80	4.70	2,898
								9	0.99	18	2.80	5.00	3,328
								10	0.95	24	2.90	4.80	2,830

APPENDIX 3

THE PHYSIOGNOMIC FACTORS AND CLASSES USED IN THE GUTIERREZ SITE-QUALITY ASSESSMENT MODEL (FROM GUTIERREZ, 1991)

Factor	Class	Scale
Climate/topography	Heat	cool
		cool-warm
		warm-cool
		warm
	Slope position	summit
		shoulder
		backslope
		footslope
		gradient <2%
		floodplain
	Slope shape	convex (dry)
		straight
		concave (wet)
		undulating
	Aspect	north
		east
		south
		west
Soil	Texture	very fine clay
		fine clay
		fine silty
		loam
		coarse silty
Past land use	Organic matter	low <3%
		medium 3-10%
		high >10%
	Compaction	<15 cm on penetrometer
		otherwise
	Moisture	wet
		moist
		dry

APPENDIX 4

THE TABLES AND EQUATIONS FOR CALCULATING THE SYNECOLOGICAL SCORES OF MOISTURE, NURIENTS, HEAT AND LIGHT FOR PLOTS IN THE TROPICAL MOIST FOREST PREMONTANE LIFE ZONE (FROM GUTIERREZ, 1991)

Table 1. Calculating the moisture synecological score for the Tropical Moist Forest Premontane Life Zone (Gutiérrez and Mize, 1993)

Factor	Class	Add
Soil	Iw Eu Ut	59
	Ah	0
Heat	Warm-cool	-41
	Anything else	0
Slope position	Footslope	49
	Otherwise	0
Soil texture	Fine clay	33
	Fine silty	36
	Otherwise	0
Soil OM	<10%	18
	>10%	0
Soil Moisture	Moist	30
	Otherwise	0
		+ 197/100=___

M=1.966+0.589(soil)-0.408(heat)+0.491(slope)+0.332(texture A)+0.362(texture B) +0.176(organic matter)+0.297(moisture)

Table 2. Calculating the nutrient synecological score for the Tropical Moist Forest Premontane Life Zone (Gutiérrez and Mize, 1993)

Factor	Class	Add
Soil	Iw Eu Ut	62
	Ah	0
Heat	Warm-cool	-42
	Anything else	0
Slope position	Footslope	49
	Otherwise	0
Soil texture	Fine clay	31
	Fine silty	34
	Otherwise	0
Soil OM	<10%	19
	>10%	0
Soil moisture	Moist	27
	Otherwise	0
		+197/100=___

N=1.974+0.621(soil)-0.425(heat)+0.487(slope)+0.309(texture A)+0.339(texture B) +0.188(organic matter)+0.274(moisture)

Table 3. Calculating the heat synecological score for the Tropical Moist Forest Premontane Life Zone (Gutiérrez and Mize, 1993)

Factor	Class	Add
Soil	Iw Eu Ut	-36
	Ah	0
Heat	Warm-cool	36
	Anything else	0
Slope position	Footslope	-47
	Otherwise	0
Site aspect	NE-SE	19
	Otherwise	0
Soil texture	Fine silty	-21
	Otherwise	0
Soil OM	<10%	-24
	>10%	0
Soil moisture	Moist	-31
	Otherwise	0
		+366/100=___

H=3.664-0.363(soil)+0.358(heat)-0.471(slope)+0.192(aspect)-0.207(texture)
-0.237(organic matter)-0.308(moisture)

Table 4. Calculating the light synecological score for the Tropical Moist Forest Premontane Life Zone (Gutiérrez and Mize, 1993)

Factor	Class	Add
Soil	Iw Eu Ut	-79
	Ah	0
Heat	Warm-cool	69
	Anything else	0
Soil depth	Shallow	-35
	Otherwise	0
Soil moisture	Moist	-38
	Otherwise	0
		+411/100=___

L=4.115-0.789(soil)+0.687(heat)-0.346(depth)-0.385(moisture)

APPENDIX 5

DATA FROM THE TWENTY-FOUR PAIRED PLOTS USED IN THE GUTIERREZ MODEL AND THE SYNECOLOGICAL SCORES CALCULATED USING THE MODEL

Plot	Soil	Slope position	Site aspect	Soil texture	Soil depth	Soil OM	Soil moisture	Moisture	Nutrient	Heat	Light
1F	Iw	Backslope	North	Loam	Deep	9	Moist	2.63	2.63	3.11	3.63
1P	Iw	Backslope	North	Loam	Deep	5.8	Dry	2.33	2.36	3.42	4.01
2F	Ut	Backslope	North	V. Fine Clay	Deep	11	Moist	2.78	2.75	3.35	3.63
2P	Ut	Backslope	North	V. Fine Clay	Deep	6.6	Dry	2.66	2.67	3.42	4.01
3F	Iw	Shoulder	North	Fine Clay	Deep	10.8	Moist	2.78	2.75	3.35	3.63
3P	Iw	Shoulder	North	Fine Clay	Deep	6.6	Dry	2.66	2.67	3.42	4.01
4F	Ut	Footslope	North	Loam	Shallow	13.2	Moist	2.94	2.93	2.88	3.28
4P	Ut	Footslope	North	Loam	Shallow	14.6	Dry	2.64	2.66	3.19	3.66
5F	Ut	Shoulder	East	V. Fine Clay	Deep	7.2	Moist	2.96	2.94	3.30	3.63
5P	Ut	Shoulder	East	Loam	Deep	8.2	Dry	2.33	2.36	3.61	4.01
6F	Ut	Backslope	North	Loam	Mod. Deep	7	Moist	2.63	2.63	3.11	3.63
6P	Ut	Backslope	North	Loam	Mod. Deep	9.8	Dry	2.33	2.36	3.42	4.01
7F	Ut	Shoulder	North	V. Fine Clay	Mod. Deep	8.2	Moist	2.96	2.94	3.11	3.63
7P	Ut	Shoulder	North	V. Fine Clay	Shallow	5.4	Dry	2.66	2.67	3.42	3.66
8F	Ut	Shoulder	North	Loam	Mod. Deep	9	Moist	2.63	2.63	3.11	3.63
8P	Ut	Shoulder	North	Loam	Mod. Deep	7	Dry	2.33	2.36	3.42	4.01
9F	Ut	Backslope	North	Loam	Mod. Deep	7.8	Moist	2.63	2.63	3.11	3.63
9P	Ut	Backslope	North	Loam	Mod. Deep	10.6	Dry	2.15	2.17	3.66	4.01
10F	Ah	Shoulder	East	V. Fine Clay	V. Shallow	11.6	Moist	2.19	2.13	3.90	4.42
10P	Ah	Shoulder	East	V. Fine Clay	V. Shallow	7.4	Dry	2.07	2.05	3.97	4.80
11F	Ah	Backslope	North	V. Fine Clay	Deep	8.6	Moist	2.37	2.32	3.47	4.42
11P	Ah	Backslope	North	V. Fine Clay	Deep	6.4	Dry	2.07	2.05	3.78	4.80
12F	Ah	Backslope	East	Loam	Mod. Deep	9.2	Moist	2.04	2.01	3.66	4.42
12P	Ah	Backslope	East	Loam	Mod. Deep	10.4	Dry	1.56	1.55	4.21	4.80
13F	Ut	Gradient <2%	None	Loam	Deep	6.4	Moist	2.63	2.63	3.11	3.63
13P	Ut	Gradient <2%	None	Loam	Deep	8.4	Dry	2.33	2.36	3.42	4.01
14F	Ut	Backslope	West	Loam	Mod. Deep	6.6	Moist	2.63	2.63	3.11	3.63
14P	Ut	Backslope	West	Loam	Mod. Deep	5.4	Dry	2.33	2.36	3.42	4.01
15F	Ut	Footslope	North	Loam	Deep	9.6	Moist	2.63	2.63	3.11	3.63
15P	Ut	Footslope	North	Loam	Deep	4	Dry	2.33	2.36	3.42	4.01
16F	Ut	Backslope	West	Loam	Mod. Deep	4.8	Moist	2.63	2.63	3.11	3.63
16P	Ut	Backslope	West	Loam	Mod. Deep	4.2	Dry	2.33	2.36	3.42	4.01
17F	Ah	Gradient <2%	East	Loam	V. Shallow	12.8	Moist	1.86	1.82	3.90	4.42
17P	Ah	Gradient <2%	East	Loam	V. Shallow	6.8	Dry	1.74	1.74	3.97	4.80
18F	Ah	Backslope	North	V. Fine Clay	Deep	9.6	Moist	2.37	2.32	3.47	4.42
18P	Ah	Backlsope	North	Loam	Deep	7.8	Dry	1.74	1.82	3.78	4.80
19F	Ah	Shoulder	South	Loam	V. Shallow	8.4	Moist	2.04	2.01	3.66	4.42
19P	Ah	Shoulder	South	Loam	V. Shallow	5.2	Dry	1.74	1.74	3.97	4.80
20F	Ut	Backslope	South	Loam	Shallow	4.6	Moist	2.63	2.63	3.11	3.28
20P	Ut	Backslope	South	Loam	Shallow	5.2	Dry	2.33	2.36	3.42	3.66
21F	Ut	Backslope	South	Loam	Shallow	5.8	Moist	2.63	2.63	3.11	3.28
21P	Ut	Backslope	South	Loam	Shallow	6.6	Dry	2.33	2.36	3.42	3.66
22F	Ut	Backslope	West	Loam	Shallow	6	Moist	2.63	2.63	3.11	3.28
22P	Ut	Backlsope	West	Loam	Shallow	5.4	Dry	2.33	2.36	3.42	3.66
23F	Ut	Backslope	North	Loam	Shallow	4.4	Moist	2.63	2.63	3.11	3.28
23P	Ut	Backslope	North	Loam	Shallow	4.8	Dry	2.33	2.36	3.42	3.66
24F	Ut	Backlsope	North	Loam	Shallow	3.6	Moist	2.63	2.63	3.11	3.28
24P	Ut	Backslope	North	V. Fine Clay	Shallow	3.4	Dry	2.66	2.67	3.42	3.66